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UNIVERSITY OF ALBERTA

LATITUDE, PHYSIOLOGICAL TIME, AND THE SPRUCE BUDWORM

BY

JAMES DAVID WEBER ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL 1994

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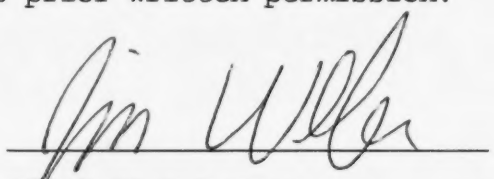

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Latitude, Physiological Time, and the Spruce Budworm, submitted by James David Weber in partial fulfilment of the requirements for the degree of Master of Science in Entomology.

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July 28, 1994

Abstract

The range of the spruce budworm, *Choristoneura fumiferana* (Clem.)(Lepidoptera: Tortricidae) is coincident with the Boreal Forest in western Canada. Spruce budworm is also found in disjunct white spruce stands south of the Boreal forest zone in Alberta. This range spans 15 degrees of latitude, from the Cypress Hills in southern Alberta to the Arctic Circle. Observed regional differences in budworm phenology led to an investigation of intrinsic development rates for populations across this gradient of latitude. Individuals from six outbreak populations were reared at ten constant temperatures from 9 to 33°C, under a photoperiod of 16L:8D. When development rates were described by a nonlinear equation, rate parameters were consistent between populations. Thus, differences in temperature-dependent development rates are not responsible for differences in phenology between budworm populations at different latitudes. The day-degrees required for spruce budworm to complete development are variable between geographic locations and between years. Bias in calculating day-degrees from daily versus hourly temperatures also varied with respect to location and year, but could not account for differences in thermal constants. Deviation of development rates from linearity at temperature extremes also fails to account for regional differences in thermal constants. A nonlinear physiological time model and a linear day-degree model produce similar development profiles for annual temperature regimes at northern and southern locations. These results reveal limitations of phenological models based solely on ambient temperature.

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Introduction

Background

The spruce budworm, *Choristoneura fumiferana* (Clem.),(Lepidoptera: Tortricidae), is a defoliator of softwood trees. Its primary hosts are white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.), and its range appears coincident with these species across North America (Harvey, 1985), throughout the Boreal forest as well as the Great Lakes-St. Lawrence and Acadian forest regions (Rowe, 1972). Spruce budworm also defoliates red spruce (*Picea rubens* Sarg.) and black spruce (*Picea mariana* (Mill.) B.S.P), and is occasionally found on pine (*Pinus* spp.) and larch (*Larix laricina* (Du Roi) K. Koch) within its range (Volney, 1989).

The spruce budworm is univoltine, and second instar larvae (L2) emerge from overwintering sites in May to feed on the developing shoots of their hosts. Early instars mine swelling buds, staminate flowers and old needles (Morris, 1963). As buds begin to flush, larvae feed on the new foliage. As shoots flare, larvae become exposed, so later instars construct feeding tunnels by webbing together cut needles and adjacent shoots. The sixth and final larval instar (L6) consumes the most foliage and completes development about the time of shoot lignification, which occurs in June (Volney & Cerezke, 1992).

Pupation lasts about two weeks, after which moths emerge and immediately mate. Females deposit ~200 eggs over a period of one or two weeks, in masses of ~20 eggs which are laid on individual needles. Oviposition sites tend to be foliage on the periphery of the crown. After about two weeks, first instar larvae hatch and disperse within the

tree crown (Régnière & Fletcher, 1983) to locate suitable overwintering sites under bark scales, flower bracts, and in lichen. Larvae spin silken hibernacula and then moult to the second instar which will undergo a winter diapause and emerge the next spring to feed and complete development.

At endemic population levels the spruce budworm is hardly detectable, but during periodic epidemics, host trees may be completely stripped of new foliage. Damage to trees defoliated by the spruce budworm is dependent on the intensity and duration of outbreaks. Severe defoliation over consecutive years results in a progressive decline of tree health. The first year may kill flowers and cone crops, followed in subsequent years by rootlet mortality, radial growth loss and some top kill (Witter et al., 1984). Tree mortality may be evident in the fifth year of an infestation, and the proportion of trees killed increases as outbreaks persist. Periodic outbreaks are extensive and persist from five to fifteen years, making spruce budworm the most destructive forest insect in North America (Volney, 1989). Volume loss averaged 42.5 million cubic metres per year in eastern Canada from 1978 to 1982 (Witter et al., 1984). This represents a substantial loss in potential revenue to the forest industry, and is the impetus for numerous research projects and management operations.

Models of Phenology

Tracking budworm phenology is valuable in timing the application of control procedures, sampling for ecological studies, and modelling population dynamics (Régnière, 1982). Phenological models allow prediction of development based on past observations, and may be most useful when population densities are low and development is difficult to track via regular sampling (Cameron et al., 1968). Dennis et al.

(1986) adapted a phenology model developed for balsam fir (Osawa et al., 1983) to describe western spruce budworm development. This stochastic model presents relative proportions of discrete developmental stages against a physiological time scale of day-degrees. Day-degrees represent the extent and duration that temperatures exceed a theoretical development threshold. The stochastic model is an improvement over previous day-degree models (Bean & Wilson, 1964; Cameron et al., 1968), as it represents a population's age structure for given day-degree accumulations, as well as the average day-degree accumulations to peak development of particular life stages.

Other phenology models which account for this variability in the duration of particular life stages have been developed and applied specifically to spruce budworm. Hudes and Shoemaker (1988) propose a model which is flexible in terms of the number of factors which can be considered, such as the effects of region, host, choice of linear or nonlinear rate curves, and others. In their model, phenology is a function of temperature inputs and calendar dates, which is interesting because thermal summation models were developed in response to the limitations of using average calendar dates to predict development events. One limitation of this model is that it fails to track adult emergence. Another is that increasing the number of parameters in a model increases the difficulty of applying it in an operational rather than theoretical context, and tends to make a model specific to the geographic region for which it was developed. Régnière (1982) proposes a multiparameter process-oriented model, which depends on maximum and minimum daily temperatures as inputs, and incorporates nonlinear development rates, variable second instar emergence, sex effects, microclimate effects, and mortality and natality factors. Régnière (1982) admits that

computational complexity precludes the model's use in general budworm management. The limitations of these budworm models have led to implementation of the stochastic model (Dennis et al., 1986) to describe spruce budworm phenology in eastern (Lysyk, 1989) and western Canada (Volney & Cerezke, 1992).

Important phenological differences in plant and insect species are commonly observed across environmental gradients. For example, the mangrove tree, *Avicennia marina*, exhibits clinal variation in timing of flowering and fruit maturation over a large (~29°) range of latitude (Duke, 1990). Regional populations of the European corn borer, *Ostrinia nubilalis*, require a broad range of day-degrees to complete development over a relatively short range of altitude in southern Alberta (~315 m)(Lee & Spence, 1986) and within the state of Pennsylvania (~260 m)(Calvin & Song, 1994). The range of the spruce budworm spans 20° latitude from southern Maine to the Arctic Circle (Harvey, 1985). Stochastic phenology models for populations over a portion of that range reveal that fewer accumulated day-degrees are required for development at higher latitudes (Volney & Cerezke, 1992). One explanation for this variation in day-degree accumulations is that intrinsic rates of development for the spruce budworm are higher at northern latitudes.

Models of Development Rate

The relationship between insect development rates and temperature is often determined by constant temperature rearing in a laboratory. When development rates are plotted against rearing temperatures, a curve results which is essentially linear over most of the range of insect development, but departs from linearity at temperatures near upper and lower thermal limits. The biophysical model of

Sharpe and DeMichele (1977) offers a theoretical basis for this nonlinearity.

The biophysical model (Sharpe and DeMichele, 1977) is based on the assumption that development rates of poikilotherms are controlled by a rate limiting enzyme. Development rates are then based on probabilities that the enzyme is either active, in a state of low temperature inactivity, or in a state of high temperature inactivity. Wagner et al. (1984) adapted the original model and redefined some of the original model parameters to simplify their estimation. The development rate at 25°C assuming 100 percent enzyme activation (RHO25), and the enthalpy of activation for the catalyzed reaction (HA), define the linear portion of the development rate curve. Modelling development at each temperature extreme requires two additional parameters to define the nonlinear portions of the rate curve. These are the temperature of 50% inactivation and the change in enthalpy associated with this inactivation. Thus, six parameters are needed to define the rate curve over a range of temperatures which includes both high temperature and low temperature inactivation.

The biophysical model of Sharpe and DeMichele (1977) warrants special consideration among nonlinear rate models as it offers a mechanism for observed rates of development. However, Lamb et al. (1984) dispute the physiological basis of this model. The assumption that a single enzyme limits developmental rate at all temperatures and throughout the development period is unlikely as different instars have different rate curves. Also, development rates are probably affected by other temperature dependent processes such as diffusion rates and phase changes of cuticular waxes. As a number of nonlinear rate models have been developed, Lamb et al. (1984) evaluated six which had been previously

published, with respect to data for egg hatch of the red turnip beetle, *Entomoscelis americana*. The preferred model was the normal equation from Taylor (1981), with parameters which have ecological rather than physiological meaning.

Taylor's (1981) rate equation is defined by three parameters, rate of maximum development (R_m), temperature of maximum development (T_m), and a spread parameter (T_o). The parameters have meaning because Taylor interprets how temperature environments affect the ecology and evolution of insect life histories, and predicts how parameters would change under different thermal conditions. Both the normal equation and the biophysical model accurately describe the effect of constant temperatures on development rates of many species (Lamb et al., 1984). Whether the physiological basis of the biophysical model is believed or disputed, the great advantage of the normal equation is that its few parameters are easily estimated by visual inspection of rate data. This is much simpler than estimating the six thermodynamic constants of a hypothetical rate controlling enzyme system. When models offer comparable accuracy in describing observed processes, ease of implementation is an important consideration (Morales-Ramos & Cate, 1993).

The nonlinear model of Taylor (1981) is also incorporated into a model of physiological time. Linear rate models are the basis for development thresholds and day-degree accumulations (Campbell et al., 1974). Such models underestimate development at temperatures near the development threshold, and overestimate it at temperatures near the upper thermal limit of development. A model of physiological time based on nonlinear development rates provides a more accurate description of development in

extreme environments, and may account for observed regional differences in day-degree accumulations for some species.

Objective

The objective of this study is to evaluate three hypotheses invoked to explain discrepancies in day-degree accumulations for the spruce budworm across its range. The first hypothesis is that intrinsic development rates vary with latitude. The second is that the method of day-degree calculations is regionally biased. The third is that development accumulation at extreme temperatures is not accurately represented by a thermal summation model based on a linear development rate curve.

To satisfy this objective, spruce budworm were first collected from populations across a gradient of latitude and reared in a laboratory at constant temperatures. Taylor's (1981) normal equation was used to describe development rates and rate curves were compared for the populations represented. Nonlinear rate curves were integrated with long term daily temperature data in Taylor's (1981) model of physiological time. Simulations of physiological time based on nonlinear and linear models were compared for two locations at extremes of the budworm's range. Hourly temperature data were used to estimate actual day-degree accumulations for different regions. These were compared to estimates from the sine method (Allen, 1976) based on daily maximum and minimum temperatures. Finally, the stochastic model (Dennis et al., 1986) was applied to additional observations of budworm phenology to determine whether regional differences in day-degree accumulations are consistent.

Bibliography

Allen, J.C. 1976. A modified sine wave method for calculating degree-days. Environ. Entomol. 5: 388-396.

Bean, J.L., and L.F. Wilson. 1964. Comparing various methods of predicting development of the spruce budworm, *Choristoneura fumiferana*, in northern Minnesota. J. Econ. Entomol. 57: 925-928.

Calvin, D.D., and P.Z. Song. 1994. Variability in postdiapause development periods of geographically separate *Ostrinia nubilalis* (Lepidoptera: Pyralidae) populations in Pennsylvania. Environ. Entomol. 23(2): 431-436.

Cameron, D.G., McDougall, G.A., and Bennett, C.W. 1968. Relation of spruce budworm development and balsam fir shoot growth to heat units. J. Econ. Entomol. 61: 857-858.

Campbell, A., B.D. Frazer, N. Gilbert, A.P. Gutierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431-438.

Dennis, B., W.P. Kemp, and R.C. Beckwith. 1986. Stochastic model of insect phenology: estimation and testing. Environ. Entomol. 15: 540-546.

Duke, N.C. 1990. Phenological trends with latitude in the mangrove tree *Avicennia marina*. Journ. Ecol. 78: 113-133.

Harvey, G.T. 1985. The taxonomy of coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): a review. *In* Recent advances in spruce budworms research. Proceedings of the CANUSA Research Symposium, 16-20 Sept. 1984. Bangor, ME. C.J. Sanders, R.W. Stark, E.J. Mullens, and J. Murphy, eds. Can. For. Serv., Ottawa, Ont.

Hudes, E.S., and C.A. Shoemaker. 1988. Inferential method for modelling insect phenology and its application to the spruce budworm (Lepidoptera: Tortricidae). Environ. Entomol. 17(1): 97-108.

Lamb, R.J., G.H. Gerber, and G.F. Atkinson. 1984. Comparison of developmental rate curves applied to egg hatching data of *Entomomoscelis americana* Brown (Coleoptera: Chrysomelidae). Environ. Entomol. 13: 868-872.

Lee, D.A., and J.R. Spence. 1986. Phenology of the European corn borer, *Ostrinia nubilalis* (Hubner), in Alberta. Can. Ent. 119: 371-380.

Lysyk, T.J. 1989. Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir. J. Econ. Entomol. 82(4): 1161-1168.

Morales-Ramos, J.A., and J.R. Cate. 1993. Temperature-dependent developmental rates of Catolaccus grandis (Hymenoptera: Pteromalidae). Environ. Entomol. 22(1): 226-233.

Morris, R.F. (ed.) 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 321 pp.

Osawa, A., C.A. Shoemaker, and J.R. Stedinger. 1983. A stochastic model of balsam fir bud phenology utilizing maximum likelihood parameter estimation. Forest Sci. 29(3): 478-490.

Régnière, J. 1982. A process-oriented model of spruce budworm phenology (Lepidoptera: Tortricidae). Can. Ent. 114: 811-825.

Régnière, J., and R.M. Fletcher. 1983. Direct measurement of spruce budworm (Lepidoptera: Tortricidae) larval dispersal in forest stands. Environ. Entomol. 12: 1532-1538.

Rowe, J.S. 1972. Forest regions of Canada. Can. For. Serv., Ottawa. Publ. No 1300. 172 pp.

Sharpe, P.J.H., and D.W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64: 649-670.

Taylor, F. 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1-23.

Volney, W.J.A. 1989. Biology and dynamics of North American coniferophagous *Choristoneura* populations. Agric. Zool. Rev. 3: 133-156.

Volney, W.J.A., and H. Cerezke. 1992. The phenology of white spruce and the spruce budworm in northern Alberta. Can. J. For. Res. 22: 198-205.

Wagner, T.L., H. Wu, P.J.H. Sharpe, R.M. Schoolfield, and R.N. Coulson. 1984. Modelling insect development rates: a literature review and application of a biophysical model. Forum: Ann. Entomol. Soc. Am. 77: 208-225.

Witter, J., D. Ostaff, and B. Montgomery. 1984. Damage assessment. In Managing the spruce budworm in eastern North America, pp. 37-64. USDA Agric. Handb. 620.

Variation of intrinsic spruce budworm development rates across a gradient of latitude.

Introduction

In western Canada, the range of the spruce budworm, *Choristoneura fumiferana* (Clem.), is approximately 15 degrees latitude, from the Cypress Hills in southern Alberta to the Mackenzie River valley at the Arctic Circle. Many species which range over such large geographic areas show regional adaptations to climate, and differentiate to the extent that separate populations are considered ecotypes (Flint, 1980). At extremes of its range, the spruce budworm must develop under different daylengths and thermal environments. Photoperiod effects are often associated with timing of synchronous events such as diapause induction (Danks, 1987) and egg hatch (Lockwood & Story, 1985), while temperature is the most important factor determining rates of insect development (Campbell et al, 1974).

Intrinsic development rates are reflected in the seasonal phenology of the spruce budworm. Phenology is usually modelled on a physiological time scale of day-degrees (Dennis & Kemp, 1986). Day-degrees are a measure of the extent to which ambient temperatures exceed a theoretical development threshold over time. Thermal constants are the accumulation of day-degrees required for completion of a given development interval, such as the interval between second instar development and moth emergence for the spruce budworm. Volney and Cerezke (1992) found that thermal constants for the spruce budworm in northern Alberta (>59 °N) are less than those determined for spruce budworm in Ontario (<50 °N)(Lysyk, 1989). An inverse relationship was apparent between thermal constants and

latitude for separate sites in Alberta, suggesting an acceleration of intrinsic development rates at northern latitudes.

Traditionally, insect development rates have been described by linear models which yield two parameters of interest to pest managers; These are development thresholds and thermal constants (Campbell et al., 1974). However, at temperature extremes the relationship of development rate to temperature is nonlinear (Sharpe & DeMichele, 1977). Taylor (1981) proposed a nonlinear normal equation to describe insect development rates as part of a larger model of physiological time based on a scale of accumulated percent development rather than accumulated day-degrees. Development accumulations, which are sums of percent development over time, arise from integration of the nonlinear development rate curve with a continuous temperature regime.

Taylor's (1981) nonlinear rate model is defined by three parameters, rate of maximum development (R_m), temperature of maximum development (T_m), and a spread parameter (T_o). Taylor (1981) predicts how rate parameters might change with an increase in latitude to accommodate a shorter growing season. An increase R_m, decrease in T_m, or an increase in T_o would lead to greater accumulations of development for a given temperature regime. Changes in R_m affect development directly and proportionately, a reduction in T_m is equivalent to increasing temperature by the same amount, and changes in T_o alter the range of temperatures over which development accumulates. Development accumulations are most sensitive to changes in R_m and T_m, especially at temperatures near the optimum (Taylor, 1982). Thus, clinal variation of intrinsic development rates of the spruce budworm would likely involve an increase in R_m or a

decrease of T_m at higher latitudes.

The first objective of this chapter is to determine if the reduction in thermal constants of spruce budworm at northern latitudes is explained by changes in intrinsic budworm development rates. The second objective is to test Taylor's (1981, 1982) hypothesis of how rate parameters might change with increasing latitude. To meet these objectives, individuals from six populations of spruce budworm across a gradient of latitude were reared in a laboratory at ten constant temperatures. Development data were described by Taylor's (1981) nonlinear development rate model. Rate curves and model parameters for the six populations are compared.

Materials and Methods

Origins of Laboratory Colonies

In June, 1992, late instar larvae were collected from spruce budworm outbreaks in the Cypress Hills (49°39'N, 110°02'W, ~1190 m above mean sea level (AMSL)) in southern Alberta, Red Lodge Provincial Park (51°57'N, 114°15'W, ~990 m AMSL) near Bowden Alberta, and Old Fort Point (64°40'N, 124°54'W, ~75 m AMSL) along the Mackenzie River, Northwest Territories (N.W.T.). Larvae were placed in 6 ml shell vials containing a plug of artificial diet on the bottom and stoppered with a wad of cotton (adapted from Thomas, 1984). Vials were then placed upside down into slots drilled in plywood trays for transportation to the laboratory in Edmonton, Alberta.

Larvae were reared to pupation at room temperature (~22°C)and 16L:8D photoperiod. Adults were paired as they emerged, and placed in 148 ml wax paper cups covered with

cheese cloth. Developing white spruce shoots were sterilized with a 1% bleach solution, rinsed, supported in shell vials filled with water, and placed in each cup to provide oviposition sites. The cotton plugs in these vials acted as wicks from which adults could sip water. Needles with egg masses were removed five and ten days after mating, placed in petri dishes sealed with parafilm beneath the lid, and incubated at ~20 °C (Robertson, 1979).

Cheese cloth squares pressed onto the bottom of the parafilm provided sites in which hibernacula could be spun (Robertson, 1979). Petri dishes were covered with black construction paper, and a small window was cut in the paper above the cheesecloth squares. The light from this window attracted larvae which then spun their hibernacula. Three weeks later, the dishes were transferred to 2 °C cabinets and held in darkness for 30 weeks. Although procedures were chosen to limit overwintering mortality and incidence of second diapause (McMorran, 1972 & 1973), field overwintering larvae were collected to supplement lab overwintering individuals.

Field overwintering larvae were collected early in 1993. 1 metre branch samples were cut from visibly damaged white spruce trees, and only those with egg casings from the previous season were kept. At least 27 branches were collected from each location (3 branches x 3 trees x 3 local stands). Samples were collected from Wrigley, N.W.T. (63°13'N, 123°29'W, ~150 m AMSL) in January, Edmonton, Alberta (53°30'N, 113°32'W, ~610 m AMSL) in February, and Big River, Saskatchewan (54°15'N, 107°25'W, ~490 m AMSL) in March. Branches were kept in an open air insectary at ambient temperatures until April, when they were brought to room temperature, forcing the second instar emergence.

Branches were tied together with string in bundles of up to six, and hung over pools of distilled water in a controlled environment chamber with RH near 100% and 16L:8D photoperiod. Bundles were grouped by location, over individual pools constructed of plastic sheets on wooden frames. Larvae wandered upwards towards overhead lights and were teased off branch ends with a fine camel hair brush. About 3 cm of bark was stripped off the branch bases to make wandering second instars (L2) more visible. Larvae also dispersed from the branches on silk, and were collected while spinning down or from the water surface. Air movement was insufficient to allow larvae to disperse between rows of branches, and petroleum jelly was used to restrict movement along the walls, ceiling, and hanging strings.

Rearing Under Constant Temperatures

Second instar larvae were placed individually on 5 ml of artificial diet in 22 ml plastic creamer cups with cardboard lids. Larvae were allowed at least two days to establish on the diet before assignment to one of ten constant temperatures. Temperature treatments were 9.3, 11.2, 13.2, 15.0, 18.5, 26.0, 29.0, 31.0, and 33.0 °C (+/- 1°C) in controlled environment cabinets. Larvae were also reared at room temperature, 24°C (+/-2°C). Control panel temperatures were corrected by thermocouple measurements of air and water temperatures within cabinets. Photoperiod was set at 16L:8D, and temperatures averaged 1°C lower during periods of darkness. Trays of water at the base of the cabinets, and moisture from the diet itself provided a humid environment for budworm rearing. Diet cups were inverted on wire mesh trays for consistent air flow around the lids, and individual trays were assigned to each population at each temperature. Trays were stacked in groups of four within the temperature cabinets and relative positions were changed

after each observation. Budworm development was monitored daily except for the three lowest temperature treatments which were monitored every second day.

Diet was prepared in 500 ml batches according to Grisdale and Wilson (1991), with the addition of 2 ml linseed oil, substitution of the B-vitamin solution with 0.6 grams of commercial lepidopteran vitamin mix, and exception of the antifungal spray. To minimize condensation, diet cups were held under paper towelling at room temperature for an hour before being stacked into freezer bags and refrigerated at 2°C until needed. Over time, diet dries and oxidizes, so cups were replaced when diet darkened and shrank. At high temperatures diet lasted a few days, while at the low temperatures it lasted up to a few weeks. Individuals were transferred without direct contact when possible by transferring the silk surrounding them, or by transferring cardboard lids when budworm were upon them. Transfers were not attempted when larvae appeared ready to moult or had just completed moulting.

Development Rate Model

Nonlinear development rates were modelled using Taylor's (1981) normal equation:

$$R(T) = R_m \exp[-0.5((T-T_m)/T_o)^2]$$

where R(T) is development rate as a function of temperature, R_m is the maximum development rate, T_m is the temperature of optimum development, and T_o represents the spread of the curve and is equivalent to the standard deviation in a normal distribution. Development rate is defined as the inverse of days required to complete development and measured as percent development per day.

Nonlinear regression was used to estimate model parameters. Marquardt's method was used in the Statistical Analysis System (SAS, 1989) nonlinear regression procedure (Proc NLIN), to calculate parameter estimates. Mean development rates for each temperature were determined. Two standard deviations above and below the mean were taken to represent a 95% prediction interval for individual rates at particular temperatures.

The output from the regression procedure includes 95% confidence intervals for the model, but further analysis using the method of Dennis et al. (1986) was necessary to determine the significance of differences in the development rate curves between developmental stages and between populations. Output from the nonlinear regression procedure includes a correlation matrix for the three parameters estimated, and parameter standard deviations. Matrix operations on these parameter correlations and standard deviations yield a multivariate statistic (W) which is used to test the null hypothesis that 3 x 1 vectors of parameter estimates from two populations are equal. As maximum likelihood estimates have normal distribution for large samples (Dennis et al., 1986), W will have a chi-square distribution with 3 degrees of freedom. The null hypothesis is rejected if W is greater than the 95th percentile of the chi-square distribution with three degrees of freedom (df)(significance level=.05). A univariate version of W is also determined to test whether individual parameters are equivalent (df=1).

Results

Constant Temperature Rearing

Second instar larvae were established on diet as

follows: 300 larvae from Wrigley, 433 from Edmonton, 367 from Big River, 330 from Old Fort Point, 432 from Red Lodge, and 160 from Cypress Hills. Survivorship to sixth instar was 55% overall, and varied between 62% for the colony from Edmonton and 47% for the one from Wrigley. As expected, the highest mortality was at temperature extremes, with larvae unable to develop at low temperatures, and dying from prolonged exposure to high temperatures. The 9.3°C treatment had the fewest individuals successfully reared to L6, with fewer than 5 individuals ($n<5$) represented in four of six populations (Table II-1). Adequate numbers survived at 33°C, but as a result of the few (160) individuals established overall from Cypress Hills, none from this population was included in this treatment. This was to ensure adequate representation of the Cypress Hills population at intermediate temperatures, so that at least the linear portion of the development rate curve could be defined. Few larvae developed to pupae (PP) at the highest temperature, so development (L3-PP) for this treatment was poorly represented in five of six populations.

Field collected larvae suffered parasitism. This was most extreme in the population from Wrigley, claiming a third of individuals at intermediate temperatures. Another problem was that other species emerged from branch samples were mistaken for spruce budworm until later instar development. Presence of the spruce coneworm, *Dioryctria reniculelloides* Mutuura & Monroe, from Wrigley and large aspen tortrix, *Choristoneura conflictana* (Walker), from Big River compounded the difficulties of low temperature rearing. Larvae from laboratory colonies were more likely to enter a second diapause, as third instars ceased feeding, spun hibernacula on the sides of the cups or on the lids, and moulted. Other larvae failed to complete moults, were ligatured by their silk webbing, or died of unknown causes.

Development Rate Model

Development rate curves (L3-L6)(Figure II-1) did not vary consistently with latitude. Development rates were highly variable as evident in the large prediction intervals at given temperatures for the colony from Edmonton (Figure II-2). Prediction intervals were of similar magnitude for individuals reared from the other locations. Confidence intervals for the model overlap between all locations for the interval L3-PP, and no population was shown to have a different rate curve ($p<=.05$) than the mean rate curve determined from pooled data (Table II-2). Values of the multivariate statistic W did increase when shorter intervals of development were considered, such as that of intermediate instar development,L3-L6, but remained below the 95th percentile of the Chi-squared distribution (Table II-2). Rate curves for Wrigley (R_m=10.5, T_m=28.6, T_o=9.6) and Cypress Hills (R_m=13.7, T_m=33.6, T_o=11.7) showed the greatest separation, though again, the null hypothesis of equality between vectors of parameter estimates was not rejected (W=4.3, p=0.23).

There were significant differences ($p<.05$) in development rates of individual instars, L3, L4, and L5, from each location as compared to mean instar specific development rates for pooled data . However, the direction of parameter deviation from estimates of the mean rate curves shows no trend with latitude, and is not consistent between instars (Table II-3). No population specific rates for the longer lived sixth instar were significantly different from the mean for pooled data.

To check for compensatory development between instars, correlation coefficients were determined for combinations of

L3, L4, L5, and L6 development rates for particular individuals, as well as combinations of early instar (L3-L5), sixth instar, and pupal development. Not all of the possible 540 coefficients were determined as a result of low survivorship at temperature extremes. Of those which were determined, only 78 had unadjusted probabilities <=0.05, and 60 of these were positive correlations. Thus, an individual developing rapidly at one interval is more likely to continue this pace at a succeeding interval rather than compensating with slower growth.

Rate curves for different instars varied in maximum development rates (R_m)(Figure II-3). Curves for L3-L4 and L4-L5 were similar (multivariate W=4.5, p=0.21), with R_m of 41.9 and 42.6%/day respectively (univariate W=0.12, p=0.73), but R_m decreases through L5-L6 (R_m=31.1%/day) and again for L6-PP (R_m=14.4%/day). Most phenology models ignore this variation and so a single rate curve for larval development is presented in Figure III-4, with parameters of the nonlinear rate model illustrated.

Discussion

The hypothesis that R_m and T_o should increase, and T_m decrease, with increases in latitude was not supported by this study. Although survival was low at extreme temperatures, the spread parameter, T_o, is the only one that would be affected by poor data for low temperature treatments, and development accumulations would be least sensitive to changes in this parameter (Taylor, 1982). Survival of larva at the highest temperatures was sufficient to determine optimum development rates which are most important for Taylor's (1981) nonlinear rate model.

The only location without representation at 33°C was

Cypress Hills, and this factor contributes to the development rate curve for this colony having the largest deviation from the mean. Cypress Hills has the highest elevation AMSL, and the site rises ~300 m in altitude over a distance of 20 kilometres as one travels south towards it. Thus, the higher altitude at this site could have confounded the effects of lower latitude. However, the rate curve (L3-L6) for budworms from this location is not different from the mean rate curve, or from those of the other colonies.

Although curves for individual instar development were different between locations, the changes in parameter estimates followed no trend with latitude and were not consistent between instars. The reversal of parameter deviations for development of different instars might be expected if compensatory development is occurring. Volney & Liebhold (1985) showed that this could occur in the development of *Choristoneura occidentalis* Freeman and *Choristoneura retiniana* (Walsingham) on artificial diet. In their study, negative correlations indicating individual developmental adjustments were more common than positive correlations between pre-emergence development, early instar development, sixth instar development, and pupal development. These would tend to reduce variation in total development time. In the field, compensatory development would function to synchronize adult emergence, and possibly facilitate resource tracking as appearance of particular instars are associated with phenological classes of host foliage (Volney & Cerezke, 1992).

It is possible that host cues or changing photoperiod could influence development in this manner. However, these conditions are lacking in the laboratory setting of this study, and there is little evidence for individual developmental adjustments in spruce budworm development on

synthetic diet. Development on diet removes many factors which could affect development in the field. Aging of foliage may be associated with changes in nutrients (Thomas, 1987), and structural changes which could influence microhabitat (Lysyk, 1989). Diet rearing does not account for feeding stimuli which may affect the rate of consumption in the field. Feeding larvae also move between buds and are affected by avoidance reactions and competition. However, these factors would not affect comparisons of intrinsic development rates between locations and between individual instars. The large intrinsic variation in these development rates may reflect great variation in selection pressure of feeding environments.

Large natural variation in development rates may allow populations to survive in years of variable host development. Several studies of defoliators on white spruce (Quiring, 1992; Turgeon, 1986; Volney & Cerezke, 1992) demonstrate a strong trend of defoliators to develop in synchrony with host tree phenology. Although this synchrony may be most important during emergence of the overwintering stage and establishment of feeding sites (Volney et al. 1983), involving pre-emergence development rates which were not studied, variation of rates during later instars could also be important if particular phenological stages of insect and host are associated.

Factors affecting development on different bud classes may be structural rather than nutritional (Quiring, 1992), and this is reflected in the timing of spruce budworm pupation which appears to coincide with shoot lignification (Volney & Cerezke, 1992). Populations reared on diet would show more variable development than those sampled in the field because they are not affected by the selection pressures of changing nutritional or physical aspects of

their diet. The changing form of developing shoots may increase budworm susceptibility to other mortality factors such as predation and parasitism. Shepherd (1992) demonstrated differential effects of mortality factors acting on the western spruce budworm (*Choristoneura occidentalis* Freeman), depending on the length of time between host bud flush and budworm pupation, when feeding larvae are exposed.

It has been observed for a number of insects, that individual instars develop at different rates (Lee & Spence, 1987). Results of this study are consistent with those published by Régnière (1987) for eastern populations of the spruce budworm. They also support field observations of shorter periods of time spent in the fifth instar relative to the sixth (McGugan, 1954), as intrinsic rates of development are higher. Of the intermediate instars (L3-L5), fifth instars appear to develop fastest in the field, and this is a result of warmer temperatures experienced by this stage relative to the third and fourth instars which have higher maximum rates of development. Masking these different development rates by a general rate curve for larval development is often a compromise of phenology models based on accumulated degree-days. However, use of more than one threshold does not necessarily improve predictions of phenology models (Kelker et al., 1990).

For insects that show physiological adaptations to latitudinal gradients, larval development rates are usually not considered, or are assumed to vary with thermal constants of phenology models. Most often, when an insect is said to develop faster in a given region, it is a reference to a lower thermal constant. For instance, Rock et al. (1993) report that the tufted apple bud moth, *Platynota idaeusalis* (Walker), and redbanded leafroller,

Argyrotaenia velutinana (Walker) develop faster at higher latitudes, based on lower thermal requirements observed for generation times in the field.

In other instances, adaptations involve diapause development and emergence times. Pschorn-Walcher (1991) examined development in six populations of the pine sawfly, *Neodiprion sertifer* (Geoff.), from a range of latitude and altitude across Europe. Samples were collected and reared under identical outdoor conditions at a single location in Switzerland. A population from southern Finland had a shorter summer diapause than that of a population from central Italy, 18° latitude to the south but of similar elevation. However, this is likely a response to photoperiod rather than thermal environment (Wallace & Sullivan, 1966). Embryonic development and larval feeding period were similar between the populations.

Trimble and Lund (1983) use the linear model to describe development rates for two populations of a mosquito, *Toxorhynchites rutilus septentrionalis* (Dyer & Knab), separated by ~9° latitude. As expected, the development threshold for the northern population was lower, but this was apparent only for the fourth instar larvae. Thresholds for overall larval development were not compared, and would likely not differ considering the pattern from this study of reduced variation of development rates between populations for longer development intervals. Tauber & Tauber (1978) found that development thresholds of the green lacewing, *Chrysopa carnea* (Stephens) decreased with increasing latitude. This is referenced by Taylor (1981) to support the hypothesis of clinal variation in rate parameters with changes in latitude. There are however, few studies which support this. This is evident in the fact that Taylor (1981) summarizes development rate parameters

from published laboratory development data for 54 species, but not one of these demonstrates a regional variation in rate parameter estimates.

The consistency of spruce budworm development rates at different latitudes suggests the rates are flexible and accommodate a range of thermal environments. It also suggests that the gradient of latitude is not isolating genotypes that are strongly selected for adaptation to local temperature regimes. This could reflect long range dispersal, of mated females. Dobesberger and Raske (1983) report moth flights of 50 to 100 kilometres, and evidence of flights between New Brunswick and Newfoundland, about 450 kilometres apart. This would cover distances between most outbreaks in western Canada, though this may be unnecessary to explain gene flow as spruce budworm is endemic throughout the boreal forest to north of the Arctic Circle. However, the apparent acceleration of development in the north reported by Shepherd (1961) and supported by Volney and Cerezke (1992), remains unexplained.

Insects at higher latitudes experience longer daylengths and reduced mean temperatures. Without investigating photoperiod, differences in phenology may be explained by a single development rate curve if the nonlinearity of this curve is having an impact on accumulated development. This is investigated in chapter three by integrating annual temperature regimes with development rate in Taylor's (1981) model of physiological time.

Table II-1. Number of individuals surviving to L6 over number established for each treatment, in order of decreasing latitude, Old Fort Point (OF), Wrigley (WR), Big River (BR), Edmonton (ED), Red Lodge (RL), and Cypress Hills (CH).

°C	Location					
	OF	WR	BR	ED	RL	CH
9.3	4/25	1/26	2/16	5/43	0/27	7/17
11.2	11/29	10/37	10/30	22/52	8/35	3/12
13.2	14/29	10/26	15/24	38/62	18/43	8/12
15.0	24/35	25/35	23/38	31/41	30/46	7/19
18.5	38/44	15/21	22/24	42/49	31/49	10/20
24.0	21/28	24/35	22/29	13/17	48/62	7/8
26.0	31/39	18/24	38/55	41/48	18/36	14/22
29.0	21/37	11/31	31/62	32/40	22/38	17/29
31.0	22/34	11/29	23/46	33/48	21/43	12/21
33.0	16/30	16/36	25/43	11/33	18/53	-

Table II-2. Comparison of development rate curves for six populations against mean rate curve for pooled data.

Location	W Statistic	
	L3-PP	L3-L6
Old Fort Point	0.03	3.41
Wrigley	0.17	3.52
Big River	1.77	5.43
Edmonton	0.72	1.98
Red Lodge	0.68	1.02
Cypress Hills	0.69	2.37

Chi(inv) = 7.81 p = .05 df = 3
Reject H_o if $W \geq 7.81$

Table II-3. Deviation of rate curve parameter estimates from mean estimates for specific instars, in order of decreasing latitude.

Location	L3-L4			L4-L5			L5-L6		
	Rm	Tm	To	Rm	Tm	To	Rm	Tm	To
Old Fort Pt.	-	.	+	+	-	.	+	.	-
Wrigley	.	.	+	-	-	.	-	.	.
Big River	.	.	+	+	+	+	-	.	+
Edmonton	+	+	-	-	.	.	+	-	-
Red Lodge	-	-	.	+	.	-	-	.	.
Cypress Hills	.	+	+	.	.	.	+	+	+

. deviation not significant (p=.05)

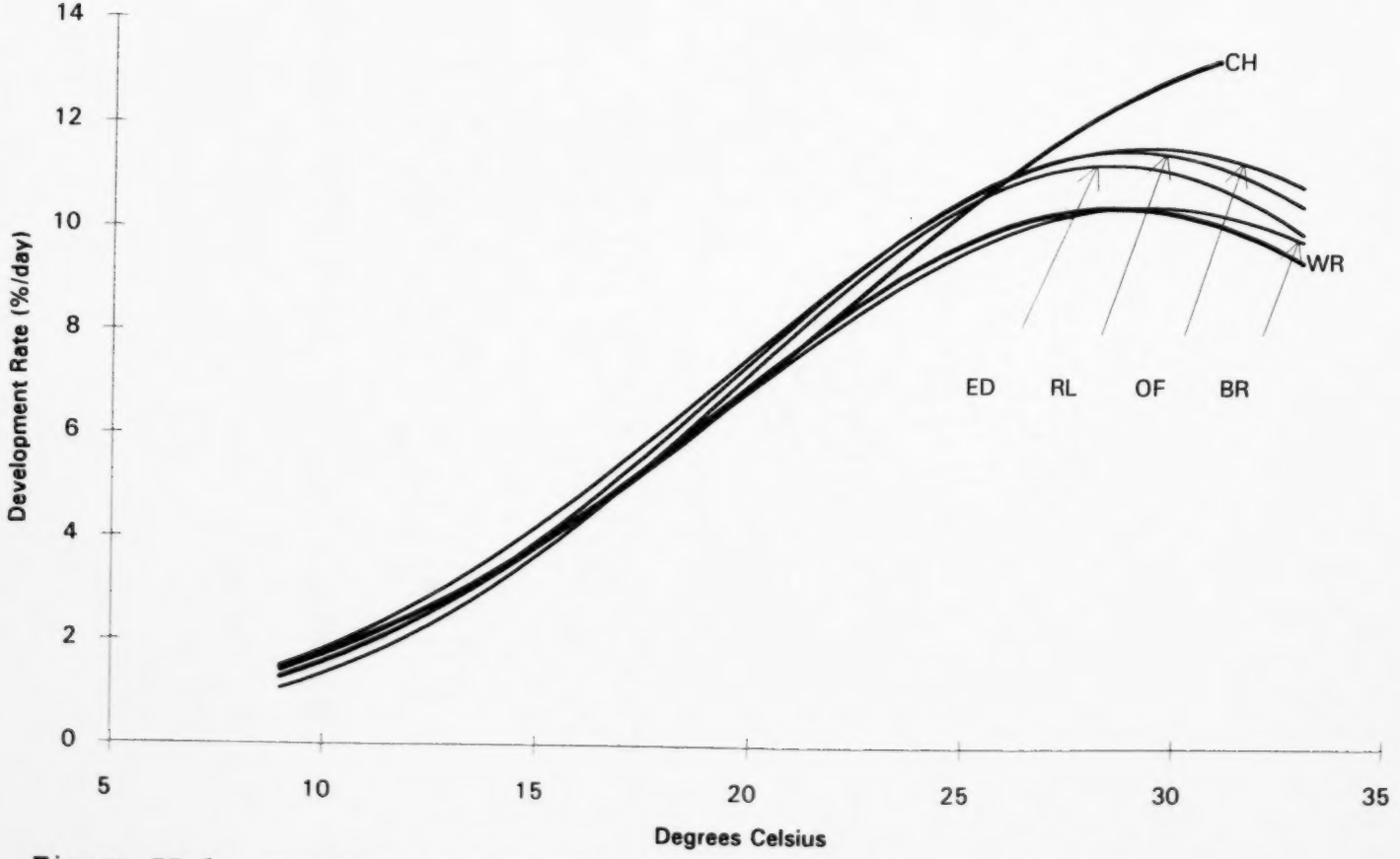

Figure II-1. Development rate, L3-L6, for six populations, with Cypress Hills (CH) and Wrigley (WR) highlighted.

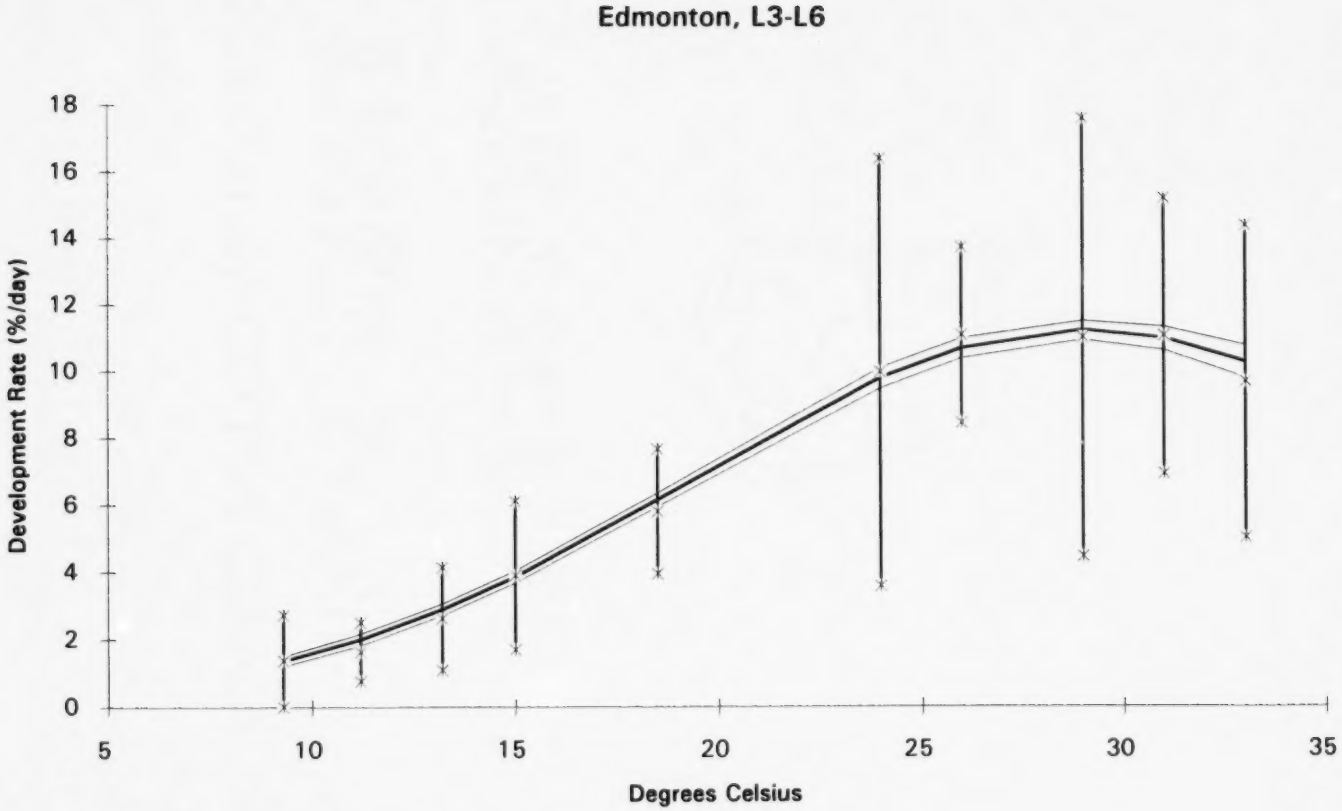

Figure II-2. Rate curve with 95% confidence intervals (model), and 95% prediction intervals (mean +/- 2 standard deviations).

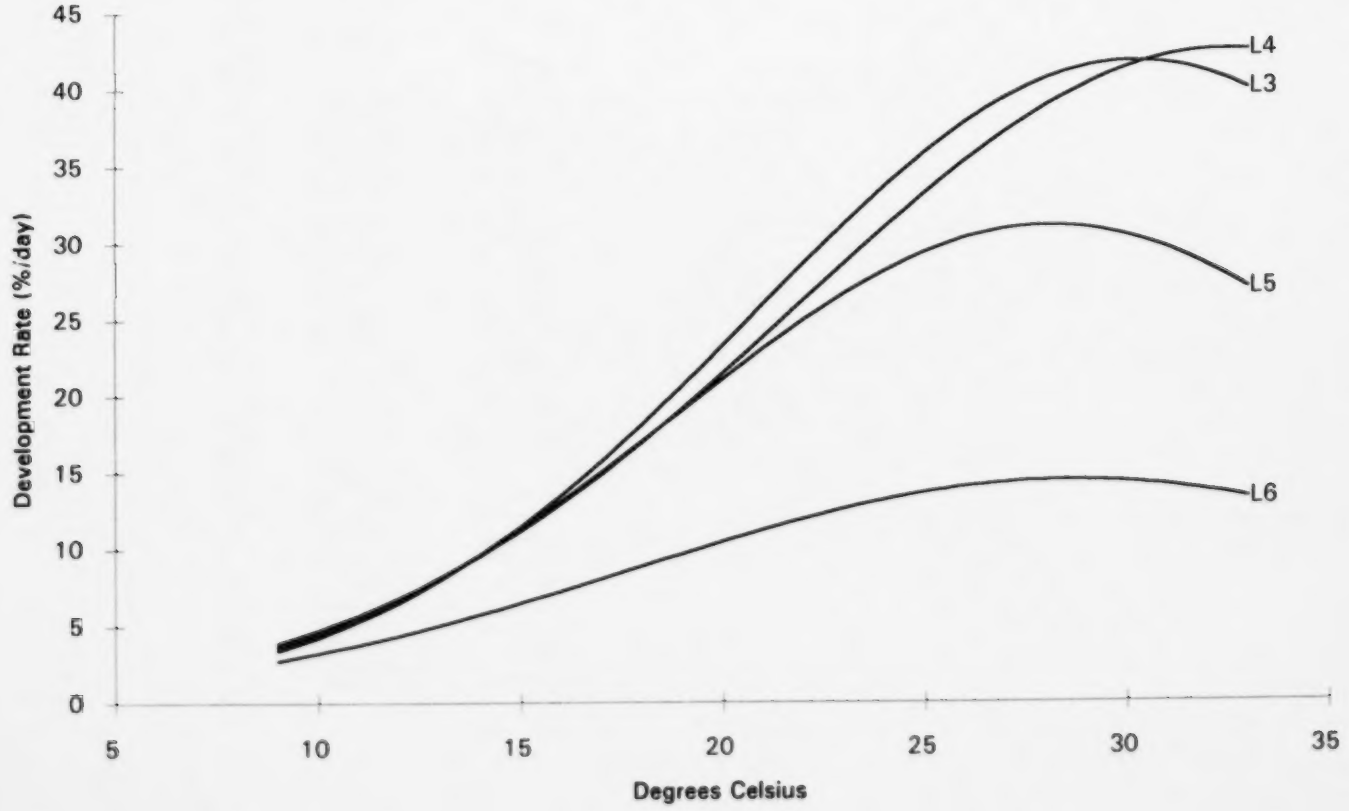

Figure II-3. Development rate for larval instars 3 through 6, pooled data.

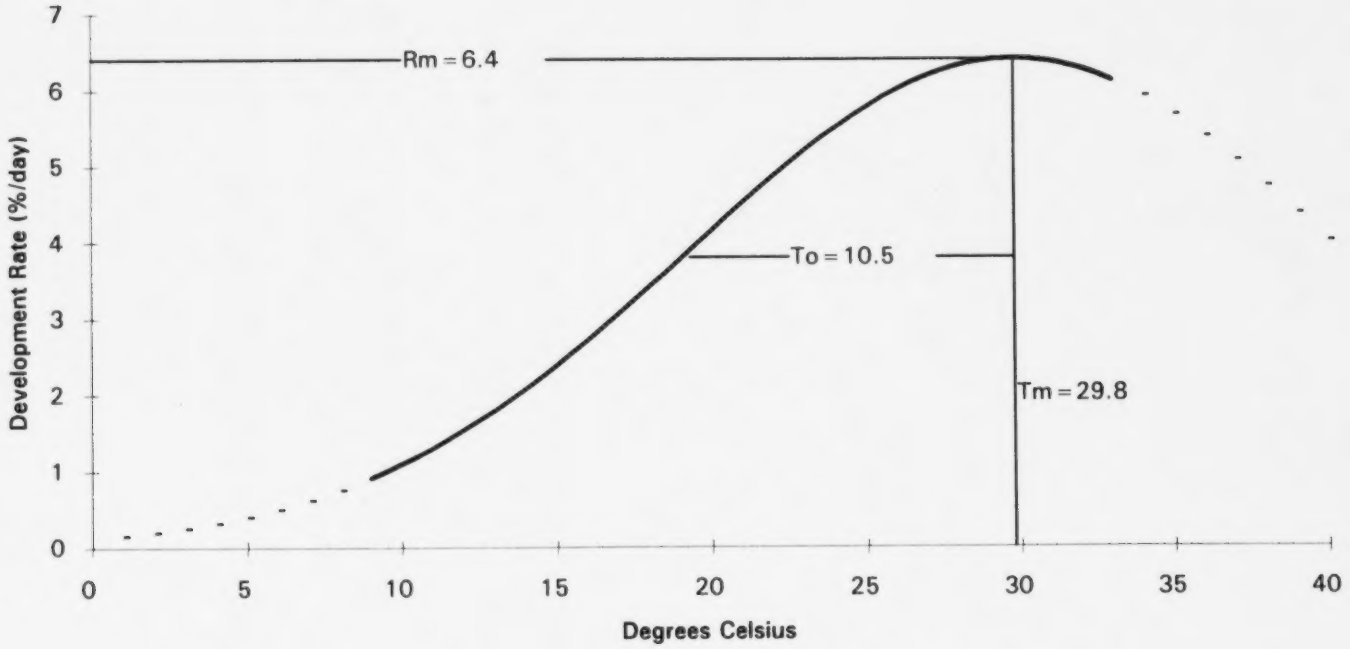

Figure II-4. Development rate, L3-Pupa, pooled data, illustrating model parameters.

Bibliography

Arnold, C.Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Am. Soc. Hort. Sci. 74: 430-455.

Campbell, A., B.D. Frazer, N. Gilbert, A.P. Gutierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431-438.

Danks, H.V. 1987. Insect dormancy: an ecological perspective. Biological Survey of Canada (Terrestrial Arthropods), Ottawa. 439 pp.

Dennis, B., W.P. Kemp, and R.C. Beckwith. 1986. Stochastic model of insect phenology: estimation and testing. Environ. Entomol. 15: 540-546.

Dobesberger, E.J., K.P. Lim, and A.G. Raske. 1983. Spruce budworm (Lepidoptera: Tortricidae) moth flight from New Brunswick to Newfoundland. Can. Ent. 115: 1641-1645.

Flint, M.L. 1980. Climatic ecotypes in *Trioxys complanatus*, a parasite of the spotted alfalfa aphid. Environ. Entomol. 9: 501-507.

Grisdale, D. 1970. An improved laboratory method for rearing large numbers of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Ent. 103: 1111-1117.

Grisdale, D. 1973. Large volume preparation and processing of a synthetic diet for insect rearing. Can. Ent. 105: 1553-1557.

Grisdale, D.G., and G.G. Wilson. 1991. Guidelines for rearing spruce budworm. Forest Pest Management Institute, Sault Ste. Marie, Ontario. 10 pp.

Harvey, G.T. 1985. The taxonomy of coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): a review. *In* Recent advances in spruce budworms research. Proceedings of the CANUSA Research Symposium, 16-20 Sept. 1984. Bangor, ME. C.J. Sanders, R.W. Stark, E.J. Mullens, and J. Murphy, eds. Can. For. Serv., Ottawa, Ont.

Kelker, D.H., D.A. Lee, and J.R. Spence. 1990. Use of standard temperature thresholds and phenological prediction for the European corn borer (*Ostrinia nubilalis* Hubner) in Alberta. Can. Ent. 122: 1247-1258.

Lamb, R.J., G.H. Gerber, and G.F. Atkinson. 1984. Comparison of developmental rate curves applied to egg hatching data of *Entomomoscelis americana* Brown (Coleoptera: Chrysomelidae). Environ. Entomol. 13: 868-872.

Lee, D.A., and J.R. Spence. 1987. Developmental adaptation of the European corn borer (Ostrinia nubilalis Hubner) in Alberta. Can Ent. 119: 371-380.

Lockwood, J.A., and R.N. Story. 1985. Photic, thermic, and sibling influences on the hatching rhythm of the southern green stink bug, *Nezara viridula* (L.). Environ. Entomol. 14: 562-567.

Lysyk, T.J. 1989. Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir. J. Econ. Entomol. 82(4): 1161-1168.

McGugan, B.M. 1954. Needle-mining habits and larval instars of the spruce budworm. Can. Ent. 86: 439-454.

McMorran, A. 1965. A synthetic diet for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. Ent. 97: 58-62.

McMorran, A. 1972. Effects of some environmental factors on the occurrence of second diapause in laboratory-reared *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Ent. 104: 1649-1653.

McMorran, A. 1973. Effects of pre-storage treatment on survival of diapausing larvae of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Ent. 105: 1005-1009.

Pschorn-Walcher, H. 1991. Development and diapause of different European provenances of the pine sawfly *Neodiprion sertifer* (Geoff.)(Hym., Diprionidae) under identical outdoor conditions. J. Appl. Ent. 112: 382-388.

Quiring, D.T. 1992. Rapid change in suitability of white spruce for a specialist herbivore, *Zeiraphera canadinsis*, as a function of leaf age. Can. J. Zool. 70: 2132-2138.

Régnière, J. 1987. Temperature-dependent development of eggs and larvae of *Choristoneura fumiferana* (Clem.)(Lepidoptera: Tortricidae) and simulation of its seasonal history. Can. Ent. 119: 717-728.

Robertson, J.L. 1979. Rearing the western spruce budworm. USDA Misc. Publ. Canada/United States Spruce Budworms Program. 18 pp.

Rock, G.C., R.E. Stinner, J.E. Bacheler, L.A. Hull, and H.W. Hogmire, Jr. 1993. Predicting geographical and within-season variation in male flights of four fruit pests. Envrion. Entomol. 22(4): 716-725.

SAS Institute Inc.. 1989. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2. Cary, NC:SAS Institute Inc., 846 pp.

Sharpe, P.J.H., and D.W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64: 649-670.

Shepherd, R.F. 1961. A comparison of the developmental rates of one- and two-year cycle spruce budworm. Can. Ent. 93: 764-771.

Shepherd, R.F. 1992. Relationships between attack rates and survival of western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), and bud development of douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Can. Ent. 124: 347-358.

Tauber, M.J., and C.A. Tauber. 1978. Evolution of physiological strategies in insects: a comparative approach with eco-physiological and genetic considerations, pp. 53-71. In H. Dingle [ed.], Evolution of insect migration and diapause. Springer-Verlag, New York.

Taylor, F. 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1-23.

Taylor, F. 1982. Sensitivity of physiological time in arthropods to variation of its parameters. Environ. Entomol. 11: 573-577.

Thomas, A.W. 1984. Individual rearing of spruce budworm larvae. Canadian Forest Service Research Notes Volume 4(2): 23-25.

Thomas, A.W. 1987. The effect of age of current-year shoots of *Picea glauca* on survival, development time and feeding efficiency of 6th-instar larvae of Chorisotneura fumiferana. Entomologia exp. appl. 43: 251-260.

Trimble, R.M. and C.T. Lund. 1983. Intra- and interpopulation variation in the thermal characteristics of preadult development of two latitudinally diverse populations of *Toxorhynchites rutilus septentrionalis* (Diptera: Culicidae). Can. Ent. 115: 659-662.

Turgeon, J.J. 1986. The phenological relationship between the larval development of the spruce budmoth, *Zeiraphera canadensis* (Lepidoptera: Tortricidae) and white spruce in northern New Brunswick. Can. Ent. 118: 345-350.

Volney, W.J.A., and H. Cerezke. 1992. The phenology of white spruce and the spruce budworm in northern Alberta. Can. J. For. Res. 22: 198-205.

Volney, W.J.A., and A.M. Liebhold. 1985. Post-diapause development of sympatric *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) and their hybrids. Can. Ent. 117: 1479-1488.

Volney, W.J.A., W.E. Waters, R.P. Akers, and A.M. Liebhold. 1983. Variation in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Ent. 115: 199-209.

Contribution of day-degree bias and nonlinear development rate curves to regional specificity of a budworm phenology model.

Introduction

Phenological models are integral to control procedures for insect pests, and to ecological studies of insects which focus on particular life stages. Lysyk (1989) applied Dennis and Kemp's (1986) stochastic phenology model and Régnière's (1982, 1987) process-oriented model to observed age distributions of spruce budworm on white spruce and balsam fir. Although observations were limited to Black Sturgeon Lake, Ontario (~49°20'N, 88°55'W), the models were tested against independent data from northern Ontario and two sites in New Brunswick. The stochastic phenology model was found to be generally applicable. The more complex process-oriented model appeared to be more regionally specific as it did not provide as good a fit to the independent data sets. However, Lysyk's (1989) parameters for the stochastic model provide grossly inaccurate predictions of budworm phenology in western Canada. Field data from northern Alberta indicate a reduction of thermal constants, day-degrees required to complete development, at higher latitudes (Volney & Cerezke, 1992). This apparent acceleration of development in northern populations was also reported by Shepherd (1961) who compared phenological observations near Fort Norman, N.W.T., to data from Cedar Lake, Ontario.

A possible explanation of this accelerated budworm development at northern latitudes is regional adaptation of intrinsic development rates. However, in chapter two, no clinal variation was found in the relationship between development rate and temperature for populations across a

gradient of latitude. Although other factors may affect development, temperature is considered the most important (Gilbert et al., 1976), and the lack of effects on rate parameters leads one to question the representation of day-degree accumulations at high latitudes. Day-degrees are usually calculated on the assumption that daily temperature traces are best approximated by a sine function between recorded maximums and minimums. Allen (1976) determined a regional positive bias in the sine method calculation which leads to overestimation of day-degree accumulations in Florida. Predicted day-degrees in Alaska tended to underestimate actual day-degrees; thus, a negative bias for northern locations might explain some of the observed differences in spruce budworm thermal constants.

Another aspect to consider is the representation of physiological time at temperature extremes. Day-degrees are one scale of physiological time, accumulated above developmental thresholds based on a linear development rate model (Arnold, 1959). However, it is accepted that observed development rates deviate from linearity near thermal limits, decreasing at high temperatures to define a thermal optimum, and remaining measurable at temperatures below the theoretical threshold of development (Sharpe & DeMichele, 1977). Taylor's (1981) model of physiological time is based on a nonlinear development rate model which is integrated with a particular temperature regime to accumulate percent development over time rather than day-degrees. Inhibition of development at high temperatures in the south, or accumulation of development at temperatures below traditional thresholds in the north, could also contribute to observed differences in thermal constants across latitude.

This chapter examines the relative impact of day-degree

bias and nonlinear development rates on a stochastic phenology model. To address day-degree bias, day-degrees were calculated directly from hourly temperature data across a latitudinal gradient and compared to those predicted by the sine method (Allen, 1976). Taylor's (1981) nonlinear development rate model was used to determine development accumulations based on temperatures from a northern and a southern location. These accumulations were compared to development predictions of a thermal summation model based on linear development rates. Finally, the stochastic model (Dennis et al., 1986) was applied to additional observations of budworm phenology to validate observed regional trends in thermal constants.

Materials and Methods

Day-degree Bias

Day-degrees were calculated using hourly temperature data from Inuvik, N.W.T. (68°13'N,134°13'W), Norman Wells, N.W.T. (65°18'N,126°42'W), and Red Deer, Alberta (52°16'N,113°48'W), for the period April-July, 1965-1992. Four years of hourly data, 1967-1970, were available for High Level, Alberta (58°31'N,117°08'W). Hourly accumulations were compared with day-degrees based on maximum and minimum daily temperatures over the same period, and on the same threshold of 6°C.

To calculate day-degrees from daily temperature data, three scenarios were considered: when the maximum is less than the threshold, no day-degrees are accumulated; when the minimum is greater than the threshold, day-degrees represent the difference between the daily average and the threshold; when daily temperatures fall above and below the threshold, day-degrees are calculated based on the area between the

sine curve approximation and the threshold (Allen, 1976). Calculations employed a single daily minimum temperature, and no upper threshold of development.

The regression procedure of the Statistical Analysis System (SAS, 1989), determined the relationship between actual day-degrees, or those based on hourly data, and predicted day-degrees, which are based on daily data. These bias equations were determined for average temperatures of each data set, and day-degree accumulations based on average data from the four locations were compared. Bias equations were then determined for individual days where the minimum temperature was above the threshold, to allow direct comparison to Allen's (1976) bias equations. Bias equations were then determined for individual years, based on days where the minimum exceeded the threshold, to examine variation of bias between years.

Physiological Time

To model physiological time and determine the effects of nonlinear growth rates on accumulated development (Taylor, 1981), annual temperature regimes were first determined from 14 to 17 year averages of daily temperatures from Ft. Norman, N.W.T. (64°54'N,125°34'W) and 27 to 29 year averages from Bowden, Alberta (51°56'N,114°02'W). These sites were chosen because they have local infestations of budworm and are close to representing the maximum range of latitude for spruce budworm in western North America (Harvey, 1985). Using mean daily data, a sine curve was defined from the maximum and minimum of each daily cycle. The sine curve for each day was then sampled ten times for each hour in the day, giving 240 point temperatures from which fractions of daily development rates were determined and then summed.

This accumulated development was then compared to day-degree accumulations estimated from maximum and minimum temperatures by the sine method. As multiple rate curves were used to represent development accumulations for different life stages, day-degrees were based on a succession of thresholds and thermal constants representing development of these same life stages. Thus, a day-degree accumulated during one stage of development is not necessarily equivalent to one accumulated during another. Thresholds and thermal constants of the day-degree model were derived from Taylor's (1981) nonlinear rate equation according to Lamb's (1992) modifications.

Lamb redefined the lower development threshold as TH_{08}, the temperature at which development rate is 8% of the maximum ($0.08R_m$) (Figure III-1), and estimated the thermal constant DD_{80}, from a line with a slope of 80% the slope of the tangent to the nonlinear curve at its inflection point. More precisely, the threshold was determined where $r=0.0831*R_m$, and the thermal constant (DD_{80}) was equal to $100T_o/0.483R_m$ (Lamb, 1992). Parameters were determined for an overall rate curve, representing third instar emergence to adult emergence (L3-A), as well as for rates of individual life stages from third instar through to pupa (Table III-1). As data on rates of second instar emergence and subsequent development were not determined in chapter two, nonlinear rate parameters were interpolated from Régnière (1987).

From Régnière (1987), maximum rates of development (R_m) equal the inverse of median development times at the published optimum temperature (T_m) of 30°C. The spread parameter (T_o) was estimated to be 10, which provided comparable fit of Taylor's (1981) rate model to that of Logan et al. (1976) which was employed by Régnière (1987).

At temperatures one standard deviation below the optimum, development rates were similar for both models. Because the shapes of rate curves vary between models, temperatures within this standard deviation required a slightly smaller T_0 to provide the best fit, while for temperatures beyond this, a larger T_0 would have been preferable. This compromise value of 10 is also within the range of values for T_0 from rate models of the other instars (Table III-1). Lamb's (1992) modified threshold and thermal constant were then derived from these nonlinear rate parameters.

When relating laboratory based development rates to field observations, it is important to consider that effects of synthetic diets can lead to discrepancies in development times. To quantify this effect, field collected second instar budworms were reared in 22 ml plastic creamer cups either on 5 ml of diet (Chapter 2; Grisdale & Wilson, 1991), or on fresh spruce foliage. Foliage was changed every second day while the median diet change was once over the period of development. The cups were kept in a cool basement, between 15 and 20°C, and out of direct sunlight. Budworms were monitored daily for instar changes.

Phenology

To determine budworm phenology at Cypress Hills, 1993, the population was sampled on Mondays, Wednesdays, and Fridays, from emergence of second instars to the end of adult eclosion. Samples were collected from three mid crown branches from each of three co-dominant white spruce. Pole pruners were used to cut 45 cm branch tips which were released over drop sheets. Larvae were removed from branch tips, and head capsule widths were used to classify them into particular instars (McGugan, 1954). This was determined by a visual comparison of head capsules against

representations of minimum head capsule widths for the third through sixth instars. Cast pupal cases were used to represent numbers of emerged adults. On average, 40 individuals were collected per sample date, reflecting a population in decline. Previously unpublished phenology data were also available from Big River, Hawk Hills, and High Level, based on samples of approximately 100 individuals per sample date. Methodology at these latter sites was the same as for Cypress Hills, except that sampling frequency increased during development of later instars, and pruners with baskets were used to collect the branches.

Phenology was modelled as in Dennis et al. (1986). Day-degrees were estimated by the sine method, from maximum and minimum temperatures recorded on site by a hygrothermograph in a Stevenson's screen. A threshold of 8°C was used to allow comparison with previously published model parameters. The nonlinear regression procedure of the Statistical Analysis System (SAS, 1989), without derivatives, was used to fit observations to the model.

Two data sets were then selected to test predictions of Lysyk's (1989) model. Linear regression of predicted average instar values against observed average instars was used for comparison. The t statistic was used to determine if regression slopes = 1 and intercepts = 0. The two data sets were then subjected to similar analyses to test model parameters derived for their specific locations of origin, but for different years' observations.

Results

Day-degree Bias

A negative bias in the sine wave approximation of day-

degrees was evident for Inuvik, Norman Wells, and Red Deer, resulting in underestimation of day-degrees for these regions. This is evident in a slope greater than one for the regression equations of predicted day-degrees against actual day-degrees (Table III-2). However the magnitude of the bias is small, resulting in a slight (<= 3.7%) deficit in accumulated day-degrees from April-July for the three locations (Table III-3). Bias does not follow a trend with latitude. The four year averages from High Level show a positive bias, resulting in a slight overestimation of accumulated day-degrees (Table III-3).

Seasonal bias equations do not improve day-degree estimations for individual days as temperature traces are highly variable. On one extreme, the broad plateau of the temperature trace about the maximum for a day in Inuvik (Figure III-2), results in a negative bias of 2.3 day-degrees as the sine approximation lies below the temperature cycle. However, another daily cycle from the same site falls well below the sine approximation, and this leads to a positive bias of 2.3 day-degrees (Figure III-3). In this instance 3.3 day-degrees are predicted, a bias of over three times the actual 1.0 day-degrees accumulated. This contrasts with the 20 percent bias from the previous figure. Thus a similar discrepancy between predicted and actual day-degrees leads to a larger bias term on a day when fewer day-degrees accumulate. This effect was taken into account by Allen (1976) who derived regression equations only from days where the temperature cycle was constantly above the threshold (Table III-4).

When regressions were based on days where the minimum exceeded the threshold temperature (Table III-4), the pattern was similar to that found for regressions based on average temperatures for all days, April-July (Table III-2).

Three locations again show a negative bias, and the few years from High Level show a positive bias. Although the slopes and intercepts have shifted slightly, there is still no trend with latitude. Larger deviations of the slopes from the line of equality would not have much affect on accumulated day-degrees as these bias equations would only be applied to portions of daily temperature traces which lie above the threshold temperature. However, average differences in day-degree accumulations would be somewhat different than the difference in day-degree accumulations based on average temperatures. The regressions reflecting a negative bias are of a lesser magnitude than the biases published by Allen (1976)(Table III-4). The slope with the largest variation from equality is from the smallest sample in both studies, which leads to an examination of the variability of regression equations among different sets of daily temperature data.

Regression slopes are highly variable between years (Table III-5). A single unusual year in High Level, 1967 (slope = 0.566), contributes to an overall positive bias. Slopes for the other three years of data from this site, 1968-1970, indicate a negative bias. All sites with a mean negative bias also show years where the bias is positive as evident from the minimum slopes which are less than 1 (Table III-5).

Physiological Time

Annual temperature regimes from Bowden and Ft. Norman show that amplitude of the annual temperature cycle increases with latitude (Figure III-4). The amplitude of the daily cycle, the difference between maximum and minimum temperatures, was similar for both sites over the period of budworm development. Larger seasonal variation of

temperatures in the north results in accumulations of heating day-degrees which lag behind those of more southern sites (Figure III-5). If the nonlinearity of development rate curves affects development times differentially between north and south, the corresponding curves of development accumulations for the two sites should approach one another. That is, the northern site should catch up in development after an initial time lag in development accumulation, or should show a reduction in the time lag to initial development.

Development accumulations were determined from development rates of three life history intervals, pre-emergence, L2-L3, and L3-A (Figure III-6). Day-degree accumulations based on successive derived thresholds and thermal constants for these three intervals (Figure III-7) reveal that the relationship between times to development for the two sites does not change with respect to choice of linear or nonlinear development model. That is, there is no reduction in the time lag of development initiation between the linear and nonlinear model, and nonlinear accumulations do not appear to close the gap in development between the two sites.

When similar comparisons are made between accumulated development and day-degrees based on 7 life history stages (Figure III-8, Figure III-9), the relationship between the curves on each figure and between figures has changed, but the end result is that nonlinear rate curves do not favour greater development accumulations for Ft. Norman as compared to Bowden. Early in the season, development accumulation from Ft. Norman does appear to be catching up to that of Bowden as the slope of the curve is greater between stage 2 and stage 5 (Figure III-8). This is reflected in the intervals of development for these stages (Table III-6),

which decrease the lag time between locations in completion dates of successive instars. However, the interval for the last two stages is longer in Ft. Norman, decreasing the slope of development accumulation. This results in a lag time of 12 days at the completion of juvenile development, versus a lag time of 13 days at the emergence of the third instars (Table III-6).

The pattern is repeated for the intervals determined from thermal summation (Table III-6), resulting in a final lag of 12 days from an initial lag of 11. It is also evident in the convergence of day-degree curves between stages 4 and 5 (Figure III-9). The increase in slopes of the day-degree curves after this point is due to lower thresholds and higher thermal constants for the final stages. The divergence of the curves after this point is due to changes in the relative temperatures experienced.

When mean temperatures are compared over the period of development (Figure III-10), Ft. Norman means are higher than those of Bowden on day 163 and stay that way for the most part, until day 198. This corresponds to the period of development L2-L6 as modelled in Ft. Norman (Table III-6). After mean temperatures drop below those of Bowden on day 198, the relative gain in development for Ft. Norman is gradually lost over the period of development L6-A.

Thermal summations were determined from the base threshold of 8°C (DD_8) for the independent simulated intervals of development (L3-A)(Table III-6). Nonlinear development has an accelerating effect on development accumulation at Bowden, as the thermal constant is smaller (~13 DD_8) for the nonlinear interval as compared to the linear one. The interval time to development, 52 days, is the same for both models (Table III-6).

The interval time to development for Ft. Norman is two days shorter for the nonlinear versus linear model (Table III-6), but the thermal constants are the same. This is a consequence of staggered initiation of development for the two models which leads to development accumulations over different periods of time. Early in the season at Ft. Norman, development accumulates below threshold values, leading to earlier predicted emergence by the nonlinear model. However, after emergence minimum average temperatures are above the development threshold. As maximum averages remain well below upper thermal limits, the nonlinear model is of no consequence.

Although nonlinear development rates do not affect development in Ft. Norman for the period represented in the model simulations, observed phenology occurs earlier in the season. Thermal constants determined from laboratory rearing on synthetic diet predict initiation of development later in the season, and predict development to be extended over a greater period of time than is observed in the field. For instance, Bowden has emergence predicted for day 152 (June 1st), at least two weeks later than would be expected, and completion of development is predicted for day 219 (August 7th), after eggs would have already hatched in the field. A comparison of development on diet versus foliage reveals that development times are more than 50% longer on synthetic diet as compared to young white spruce shoots (Table III-7).

However, a correction factor is not required to determine the relative effects of development accumulations below threshold temperatures for the two sites. The greater average accumulation of development at temperatures below threshold in Bowden would still remain if development is

earlier in the season. This is because annual temperature cycles for northern locations have a steeper slope where they cross the threshold, resulting in fewer days where temperatures border the threshold (Figure III-4). For a threshold of 8°C, consistent accumulations of day-degrees for Bowden begin on day 98, and minimum temperatures cross the threshold around day 168, 70 days later. In Ft. Norman, the respective conditions are met on day 126 and day 168, a period of 42 days.

Phenology

The stochastic phenology model for Cypress Hills, 1993, shows a very broad distribution of instars about the mean of their development, resulting in masking of the peaks for fifth instars, and pupae (Figure III-11). The model parameter which describes the spread of these curves, b^2, equals 10.1, and is the largest of all the observations modelled. A large spread parameter was determined for the High Level ,1990, model (Volney & Cerezke, 1992), and was attributed to variation between the three separate sample sites from which data were pooled to determine phenology. In this instance, a probable cause for the large spread parameter is the state of population decline. Small sample size, especially for pupae, is a result of few individuals surviving to the latter stages of development. This makes it unlikely that any one stage will be very dominant in terms of proportion of population at peak occurrence. As the appearance of one instar is declining, the numbers of subsequent instars are falling so the proportional difference is slight. Another factor is the lingering development of unhealthy individuals.

Régnière (1982) cites viral infection as a source of exaggerated variability in the distribution of later instars

in his process model. However, the peaks of instar development are more distinct, and represent a greater proportion of the population in Régnière's (1982) model than for the stochastic model (Dennis et al., 1986) as applied to populations in the west. Phenology from Big River, 1993b (one of two local sites)(Figure III-12), also reveals a compression of intermediate instar development (L3-L6), even with a moderate value of 2.9 for the spread parameter. This compression was noted by Volney & Cerezke (1992), which led to the hypothesis that increased development rates of intermediate instars resulted in smaller thermal constants for development.

Parameter estimates a_1 and a_6 represent the times when the population is 50% second instars and 50% adults respectively. The difference between these parameters is the thermal constant which is compared between models. Although these parameters are not directly comparable for the Cypress Hills observations, as temperature inputs were only available from the time of sampling, this does not affect the thermal constant (Table III-8). The thermal constant of 244.3 DD_8 is less than those determined from Big River in 1993, which goes against the expected trend with latitude. However, Cypress Hills has the highest elevation and relative altitude above the surrounding landscape of any of the western populations, so this would tend to counter latitudinal effects.

Determining any trend between sites is difficult as there are few coincident phenologies to compare model parameters from. The 1990 data show a lower thermal constant for High Level than Hawk Hills (Volney & Cerezke, 1992). The 1991 data also shows the northernmost location, High Level, with the lowest thermal constant. However, the difference in thermal constants in 1991, 7.2 DD, is much

less than the 45.2 DD difference from 1990. Thermal constants vary between years for a given location, and the relative changes for different locations do not appear to be correlated. As a result, there is no discernable latitudinal trend in thermal constants for western Canada. However, a large and consistent discrepancy exists between parameters at these locations and those defined by Lysyk (1989).

Emergence of the spruce budworm in western Canada requires consistently greater accumulations of day-degrees than that determined for Ontario, while thermal constants are consistently lower (Table III-8). Individual model parameters can be compared by using the 95% confidence intervals from the nonlinear regression procedure. All thermal constants from the western observations have confidence intervals which do not overlap those of the Ontario thermal constant (345.0 DD). If these thermal constants are pooled (excluding Ontario 1989 and substituting an average of the two constants from Big River 1993), the mean is 246.11 with a standard deviation of 26.03 (n=7). The Ontario value falls 3.8 standard deviations from the mean. Lysyk (1989) tested his model against independent data sets from Northern Ontario and New Brunswick, by comparing observed average instars with observed model predictions. The data sets from High Level, 1990, and Big River, 1993b, were chosen for such a comparison as their model parameters represent the largest and smallest deviations from those of Ontario, 1989.

When predicted average instars (x) were regressed against observed average instars (y), the result was a slope significantly greater than 1 (t, p=.05) for both sets of observations. This resulted in an overestimation of development early in the season, and underestimation of

development beyond the fifth instar for High Level (Figure III-13), and beyond the sixth instar for Big River (Figure III-14). Fit of models from High Level, 1991, against 1990 data, and Big River, 1992, against 1993 data was also poor, as regression slopes were significantly different from 1 ($p<=.05$)(Table III-9). The worst fit was of Big River 1992 model parameters on 1993 observations, which lagged behind model predictions from 1 to 2 weeks over the entire period of development. Thus, stochastic phenology models can be expected to be regional, applicable to local areas and specific only to years with very similar temperature patterns.

Discussion

The change in thermal constants for spruce budworm from east to west make it tempting to invoke some influence of latitude on development, as Lysyk's (1989) parameters were based on the most southern population considered. Shepherd (1961) also reported accelerated development at northern latitudes, when a population of spruce budworm from Norman Wells, N.W.T., 1959, was compared to one from Cedar Lake, Ontario, 1951. A visual inspection of figures 4 and 5 in Shepherd (1961) reveal a difference in thermal summations between second instar emergence and 50% moth flight of roughly 3500 degree hours farenheight (F), or 81 day-degrees celsius above a threshold of 5.6°C (42°F). This value is comparable to the average 100 DD_8 difference in thermal constants between western sites and Ontario, 1989. The differences between Lysyk's (1989) thermal constant and those characterizing western populations of spruce budworm are not resolved by either day-degree bias or nonlinear development accumulations.

Bias in calculation of day-degrees does not appear to

contribute to differences in day-degree summations across a gradient of latitude. This reinforces the conclusion of Allen (1976), who determined a positive bias for Florida and a negative bias for Alaska, but failed to find a trend with latitude when intermediate locations were considered. Although three locations in western Canada show a slight negative bias, unless locations in eastern Canada experience a large (~20%) positive bias, these errors in day-degree accumulations are not adequate to explain the observed variation in budworm thermal constants between the two regions. This study raises questions as to the usefulness of bias adjustments as determined by Allen (1976).

Methods of calculating day-degree bias differ between this study and that of Allen (1976). Temperatures for the period April-July, were chosen here to represent the period from L2 emergence to moth flight. Allen's (1976) bias equations represent 25 days from December and 25 from July, to cover the most extreme differences. Apparently these dates were collected from a single year, with actual day-degrees calculated from planimeter measures of temperature traces. Pruess (1983) determined bias in a similar manner, using temperatures from select dates in 1963, but did not publish equations as the bias parameters differed from those of Allen (1976). It was believed that using reported temperatures for calculating actual day-degrees, rather than planimeter tracings was in part responsible for this discrepancy; therefore, Pruess (1983) did not want bias parameters with inherent errors of calculation utilized. Planimeter measures and hourly calculations should be equivalent as fluctuations of the daily temperature trace above and below hourly measurements tend to cancel each other and would not be expected to influence bias in a given direction. However, taking measures from a single year fails to account for variation in bias between years, which

does lead to large differences in bias parameters, to the point of reversing the direction of bias.

Bias equations based on all days for a given period of the development year, are a measure of how overall day-degree accumulations are affected for that particular time and place. An understanding of the variation in overall differences in thermal summations is necessary, and even crude estimates of bias are preferable to the use of a more precisely determined bias which fails to account for this variation between years. Allen (1976) may have assumed this variation was because bias for a given day is dependent on the proportion of daily temperature above the threshold. The choice of days where the minimum temperature was above the threshold, implied an increase in accuracy of prediction. However, all these sources of error between bias calculations are small compared to the large variation between years. In fact, variation in bias between years was less when all days, April-July, were considered, than when only days with minimum temperatures above the threshold were considered (Inuvik, Table III-5). By including large numbers of observations over many years, this study reveals the variation which was not considered by Allen (1976) or Pruess (1983).

The reason bias is inconsistent is that the shape of individual traces is highly variable. Shepherd (1961) speculated that lower diurnal variation in temperature traces from high latitudes would affect day-degree accumulations. This was reworked by Volney and Cerezke (1992) to read that northern stations experience temperatures above the mean for more than half the day, leading to an underestimation of day-degrees at these sites (Figure III-2). This deviation from the sine curve is not consistent, nor exclusive to northern sites, as daylength

does not appear to affect regional bias. A contrasting temperature trace (Figure III-3) shows how daily temperature cycles can be interrupted by regional weather phenomena. In this instance, the continual drop in temperature from the start of the day may be the result of an advancing cold front. Such patterns are likely independent of latitude, and are responsible in part for the lack of trend in the difference between actual and estimated day-degree accumulations. Higley et al. (1986) also point out that the search for precision in day-degree calculations often fails to consider the limitations of day-degree models, which are only estimations of observed development.

Other estimations of physiological time may incorporate nonlinear development rate curves. For periods when daily temperatures fluctuate about a base threshold, nonlinear models predict greater accumulations of development than linear day-degree models. However, this does not favour differential accumulations in the Northwest Territories as compared to central Alberta. Average maximum temperatures do not approach upper thermal limits which would slow development in the south, even considering that insect microhabitats often exceed ambient temperatures by 5°C (Wellington, 1950). Maximum temperatures on individual days approach these limits but these temperatures are not sustained, and are unlikely to affect development to a large extent over a season. As for development accumulation below base thresholds, it appears that this would have a greater effect on thermal constants for south temperate populations rather than north temperate ones, due to the less severe annual temperature regimes (Figure III-4). This may explain the early emergence of second instars in Lysyk's (1989) model with respect to day-degree accumulations (parameter a_1, Table III-8). However this fails to explain the average difference in thermal constants for western populations.

Whether these thermal constants exhibit clinal variation with latitude is unclear. Variation in thermal constants between geographical locations is confounded by a number of factors, such as population decline, or unusually warm or cool temperatures in a given year. The nonlinear development accumulations below base thresholds may influence the variation between years. The small thermal constant for Big River, 1992, corresponded to below average seasonal temperatures. Linear models developed for observations from a warmer year, where nonlinear accumulations have little effect, would tend to underestimate development in this instance.

Another explanation for development variation between years and locations involves host plant effects. Host tree effects on budworm development have been modelled by Lysyk (1989) and Hudes & Shoemaker (1984), and it is clear that host selection impacts phenology, whether this is a nutritional effect, or microclimatic one (Lysyk 1989). Volney et al. (1983) propose that host phenology acts as a screen against the large intrinsic variation of budworm development rates. Thus, observations in the field may reflect differential survivorship according to the degree of host-insect synchrony. As tree development is affected by soil temperatures as well as air temperatures (Cleary & Waring, 1968), tree responses to ambient temperatures may vary geographically. If observed differences in budworm development reflect resource tracking, the differential between soil and ambient temperatures in the north may be influencing the apparent delayed emergence of second instars.

Loss of snow cover in the spring is one mechanism which could affect the relative difference between soil

temperatures and ambient temperatures between locations. For a given amount of precipitation, lower winter temperatures lead to a greater accumulation of snow pack in the north because warm spells which could melt snow cover are absent from fall to spring. As the annual temperature cycles are more severe in the north, spring warming is not as gradual as in the south, leaving less time for the snow pack to melt and ground to thaw before ambient temperatures rise above development thresholds. Thus, the greater differential between air and soil temperatures could lead to greater day-degree accumulations before budflush. However, these considerations all deal with temperature effects on development, while another factor which varies with latitude, photoperiod, remains uninvestigated.

Day-degree bias at northern locations was investigated because spring daylengths are longer at high latitudes. Elevated temperatures within feeding tunnels may be sustained for longer in the day due to the extended sunlight hours (Shepherd, 1958). Extended daylight may also affect insect activity levels (Morris & Fulton, 1970). Accelerated development might then be a product of the budworms actively feeding for more hours each day. Another consideration is that the percentage of daylight hours with bright sunshine (sunshine index) varies across different regions and may affect budworm microclimates. Whether these additional factors affect development accumulations remains to be investigated. However, whether such additional factors would improve model predictions remains open to debate. For now, temperature based phenology models allow comparison between development of populations across a wide geographic and temporal range. These comparisons raise many questions as to what factors act in concert to produce observed phenologies; thus, phenology models are a useful reference to development if limitations of the form are understood.

Table III-1. Day-degree thresholds (TH_{08}) and thermal constants (DD_{80}) derived from nonlinear rate curves for various development intervals (As in Lamb, 1992).

	Rate Parameters				
Interval	R_m	T_m	T_o	TH_{08}	DD_{80}
L3-L4	41.85	30.21	9.45	9.13	46.75
L4-L5	42.62	32.53	10.72	8.63	52.07
L5-L6'	31.12	28.10	9.20	7.57	61.24
L6-PP	14.43	28.57	10.70	4.69	153.61
PP-A	18.18	30.42	10.58	6.82	120.46
L3-A	4.79	30.58	10.91	6.25	471.23
L2'	17	30	10	7.6	121.79
L2-L3'	24	30	10	7.6	86.27

'Estimated from Régnière (1987)
L2 represents pre-emergence development

Table III-2. Regression equations of predicted day-degrees (x) against actual day-degrees (y), average daily temperatures, April-July, 1965-1992.

Location	Equation
Inuvik	y = 0.004 + 1.037x
Norman Wells	y = -0.017 + 1.021x
High Level*	y = 0.255 + 0.944x
Red Deer	y = 0.043 + 1.023x

Threshold = 6°C
R-square > 0.99, n = 122
*Based on four year averages, R-square > 0.96

Table III-3. Day-degree accumulations, based on hourly and daily average temperatures, April-July, 1965-1992.

Location	Hourly	Daily	Difference
Inuvik	453.9	437.1	16.8
Norman Wells	692.3	680.5	11.8
High Level*	667.5	674.1	-6.6
Red Deer	742.7	720.6	22.1

Threshold = 6°C
*Four year average

Table III-4. Regression equations of predicted day-degrees (x) against actual day-degrees (y), for days where the minimum temperature exceeds the threshold temperature, April-July, 1965-1992.

Location	Equation	n	R^2
Inuvik	y = -0.179 + 1.056x	967	0.95
Norman Wells	y = 0.037 + 1.012x	1607	0.95
High Level*	y = 0.652 + 0.850x	165	0.57
Red Deer	y = -0.227 + 1.036x	1539	0.94
Alaska'	y = -0.859 + 1.208x	50	r = 0.916
Florida'	y = 0.206 + 0.837x	200	r = 0.902

Threshold = 6°C
*Based on four years of data
'From Allen (1976), threshold = 10°C

Table III-5. Summary statistics for regression slopes of predicted day-degrees (x) against actual day-degrees (y), for days where the minimum temperature exceeds the threshold of 6°C, April-July, individual years.

Location	mean	s	min	max	n
Inuvik	1.061	0.037	0.975	1.141	28
Inuvik*	1.047	0.019	1.014	1.095	28
Norman Wells	1.010	0.035	0.906	1.052	28
High Level	0.936	0.250	0.566	1.098	4
Red Deer	1.036	0.047	0.930	1.127	28

* includes all days, n = 122 for each year

Accumulated Development Based on Nonlinear Rate Models

	Bowden			Ft. Norman		
Stage	Dat	Interval	Stage	Dat	Interval	Lag Time
L2	146		L2	163		17
L2-L3	162	16	L2-L3	175	12	13
L3-L4	171	9	L3-L4	182	7	11
L4-L5	180	9	L4-L5	189	7	9
L5-L6	188	8	L5-L6	196	7	8
L6-PP	201	13	L6-PP	210	14	9
PP-A	214	13	PP-A	226	16	12
L3-A		52	L3-A		51	
		DD8 = 374.28			DD8 = 368.96	

Accumulated Development Based on Thresholds and Thermal Constants

	Bowden			Ft. Norman		
Stage	Dat	Interval	Stage	Dat	Interval	Lag Time
L2	152		L2	166		14
L2-L3	167	15	L2-L3	178	12	11
L3-L4	176	9	L3-L4	184	6	8
L4-L5	185	9	L4-L5	191	7	6
L5-L6	193	8	L5-L6	198	7	5
L6-PP	207	14	L6-PP	213	15	6
PP-A	219	12	PP-A	231	18	12
L3-A		52	L3-A		53	
		DD8 = 387.71			DD8 = 368.55	

Table III-6. Comparison of times to development, based on nonlinear and linear rate models.

Table III-7. Comparison of budworm development times on synthetic diet versus foliage of white spruce. Temperatures variable between 15 and 20°C.

	Days to Development, L3-PP			
Treatment	Mean	s	n	rate (%)
Diet	31.07	4.14	30	3.22
Foliage	20.63	4.10	16	4.85

Table III-8. Cumulative day-degrees (DD_8) from 50% l2 to 50% adult emergence, which is the difference between phenology model parameters a_6 and a_1 (Threshold = 8°C).

Location	year	a_1	a_6	DD_8
High Level, Ab.'	1990	108.7	317.4	208.7
Hawk Hills, Ab.'	1990	121.7	375.7	253.9
Ontario*	1989	91.7	436.7	345.0
Chinchaga R., Ab.	1991	122.9	378.2	255.5
Hawk Hills, Ab.	1991	174.5	437.2	262.7
Big River, Sk.	1992	102.3	317.8	215.5
Big River, Sk.	1993a	110.2	391.1	280.9
Big River, Sk.	1993b	103.7	387.2	283.5
Cypress Hills, Ab.	1993	-	-	244.3

*Lysyk, 1989
'Volney & Cerezke, 1992

Table III-9. Regression equations of predicted average instar (x), against observed average instar (y).

Observations	Model	Equation*
High Level, '90	Ontario, '89	$y = -0.538 + 1.105x$
	H. Level '91	$y = -0.083 + 1.054x$
Big River, '93b	Ontario, '89	$y = -1.441 + 1.225x$
	B. River, '92	$y = -0.483 + 0.959x$

*all slopes different from 1 (t, $p \leq .05$)
*Big River intercepts different from 0 (t, $p \leq .05$)

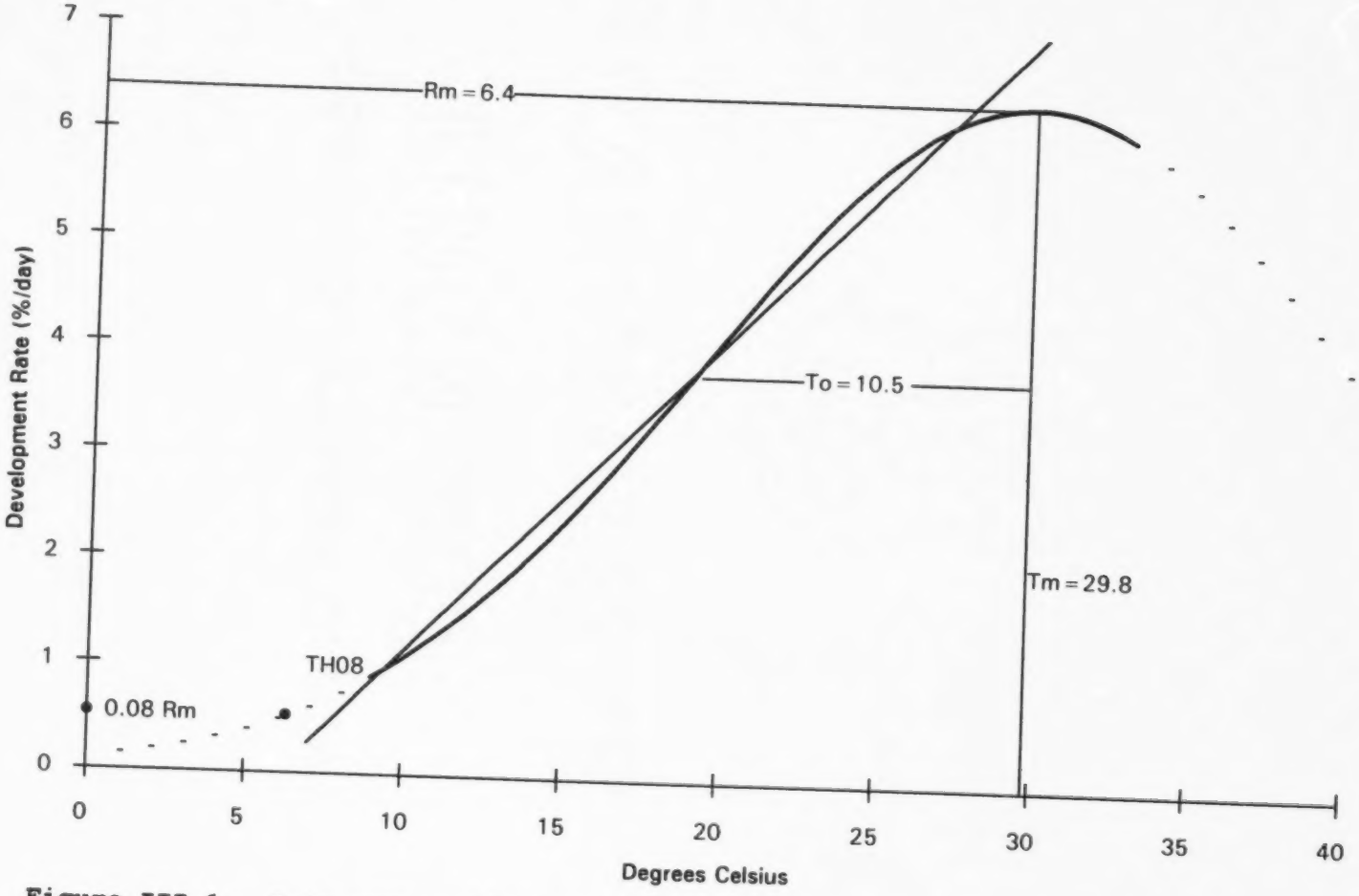

Figure III-1. Rate curve, L3-Pupa, illustrating model parameters and linear adaptation.

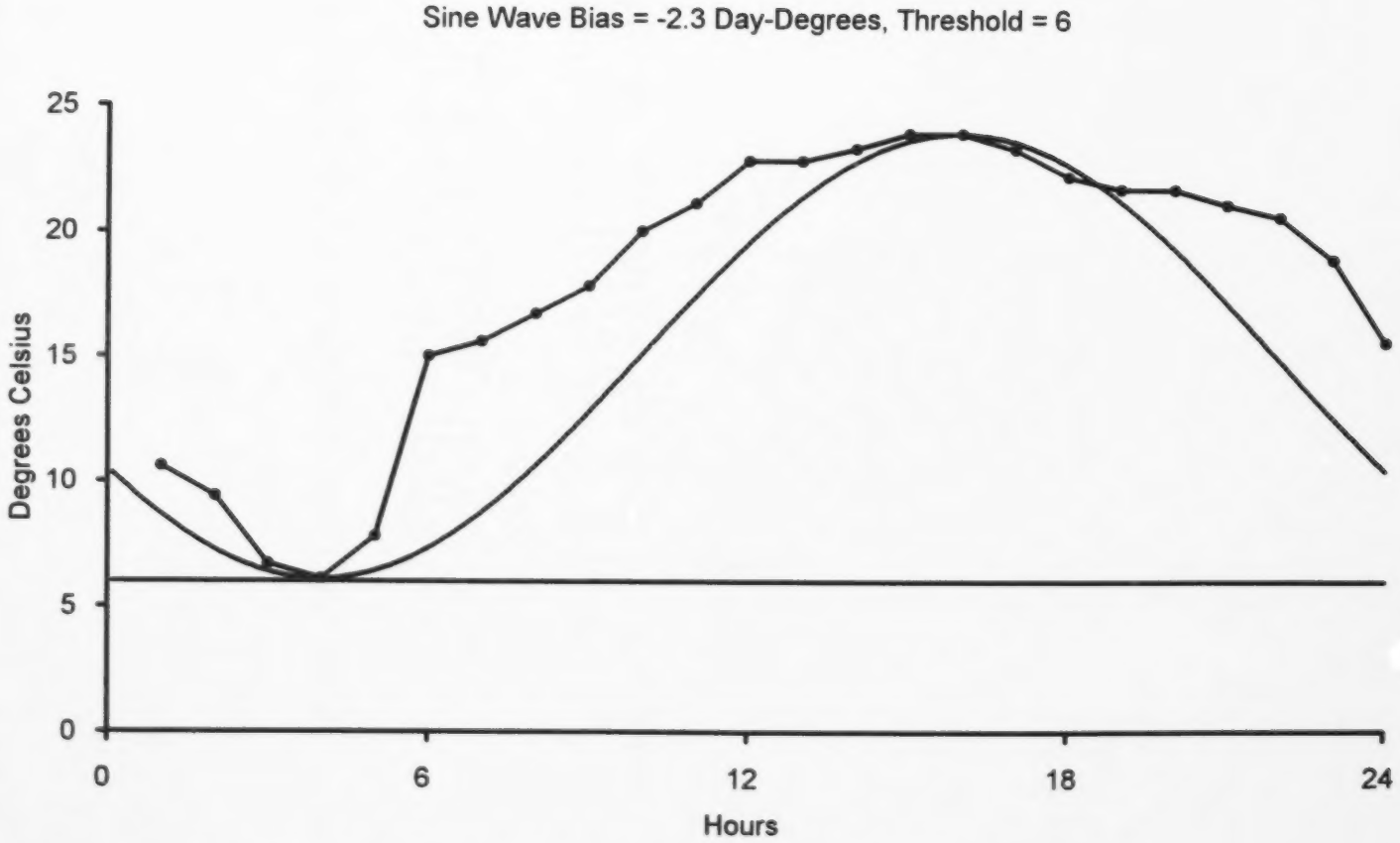

Figure III-2. Hourly temperature and sine wave estimate for Inuvik, July 19, 1967.

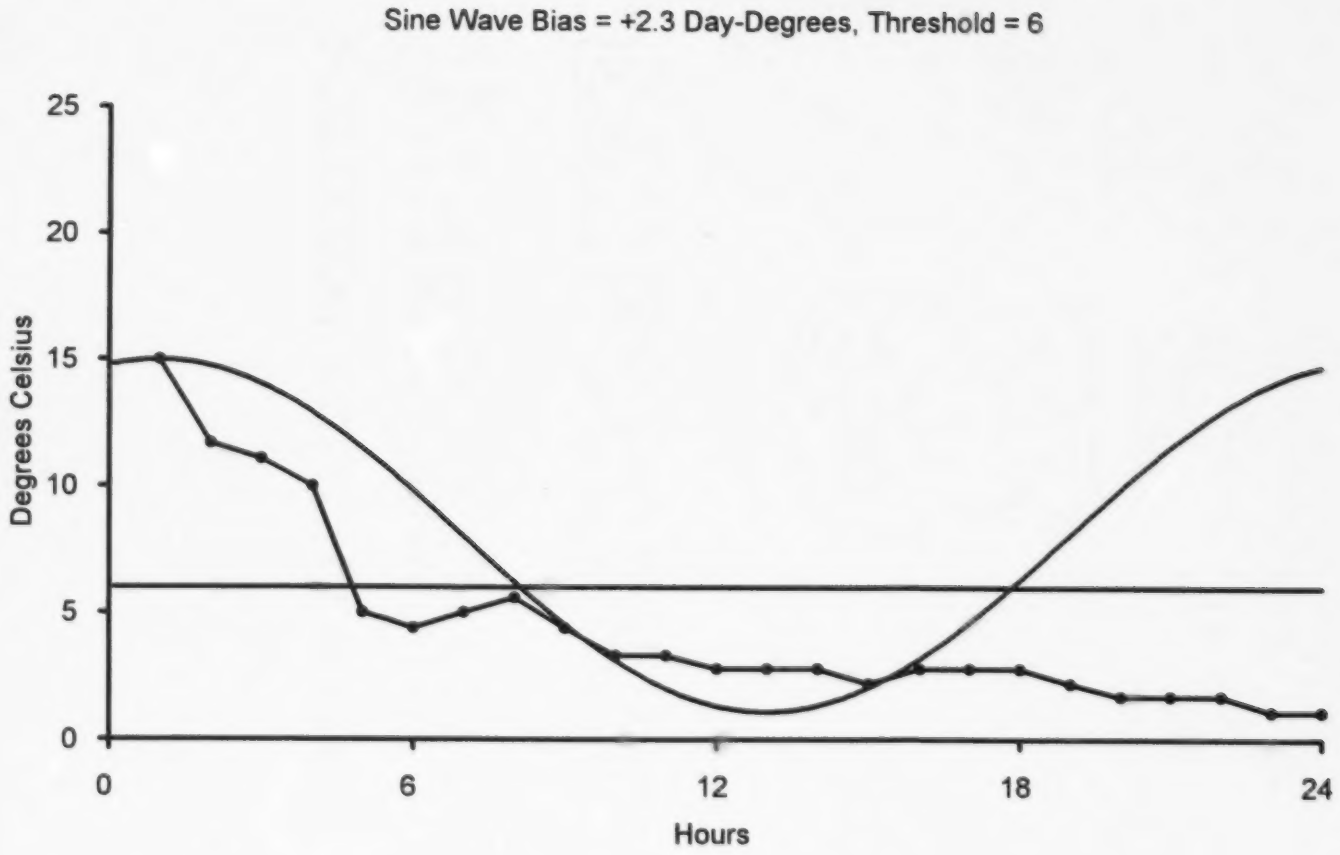

Figure III-3. Hourly temperature and sine wave estimate for Inuvik, June 9, 1967.

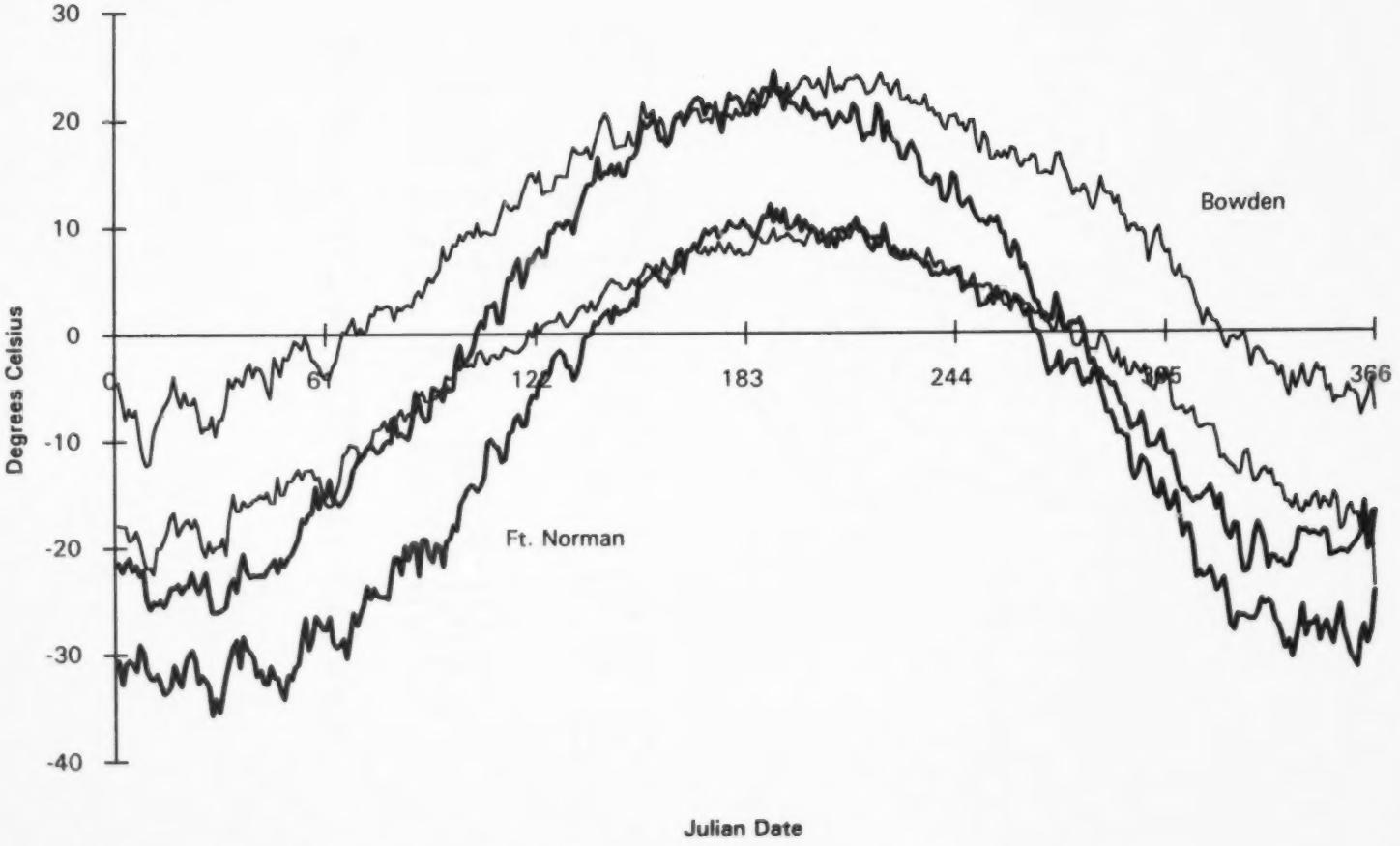

Figure III-4. Annual temperature cycles of average daily maximum and minimums.

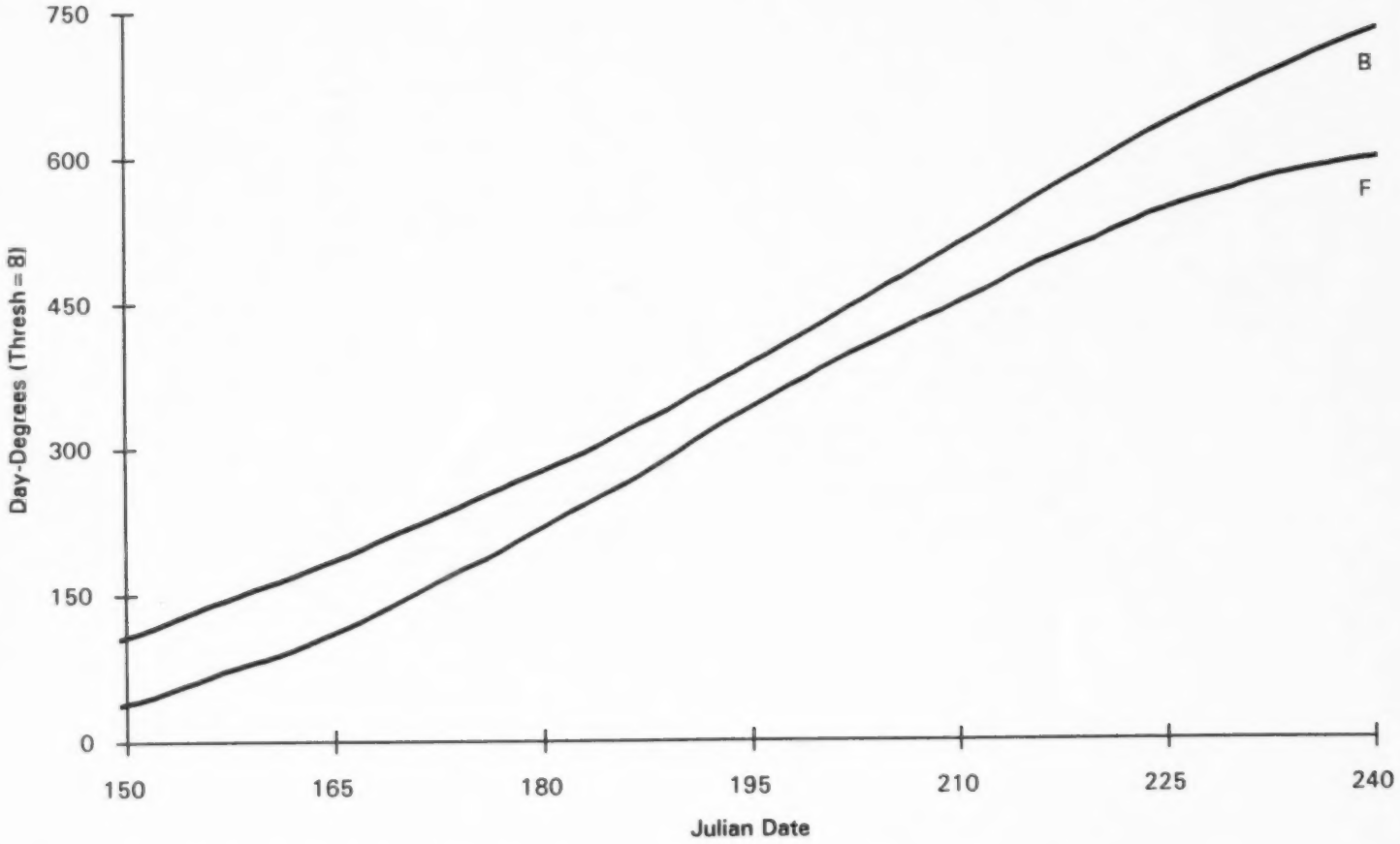

Figure III-5. Average day-degree accumulations, Bowden (B) and Ft. Norman (F).

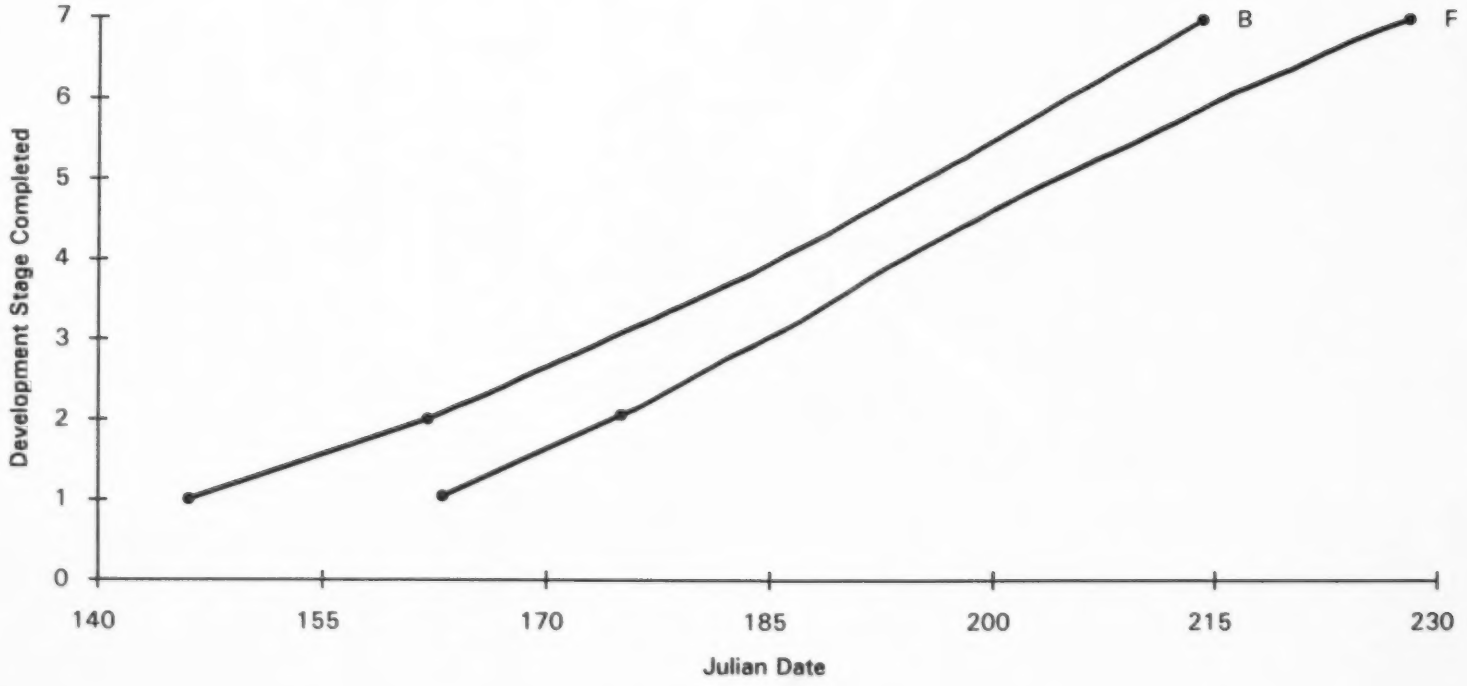

Figure III-6. Development accumulation, Bowden (B) and Ft. Norman (F), three development intervals (Emergence, L2, L3-A).

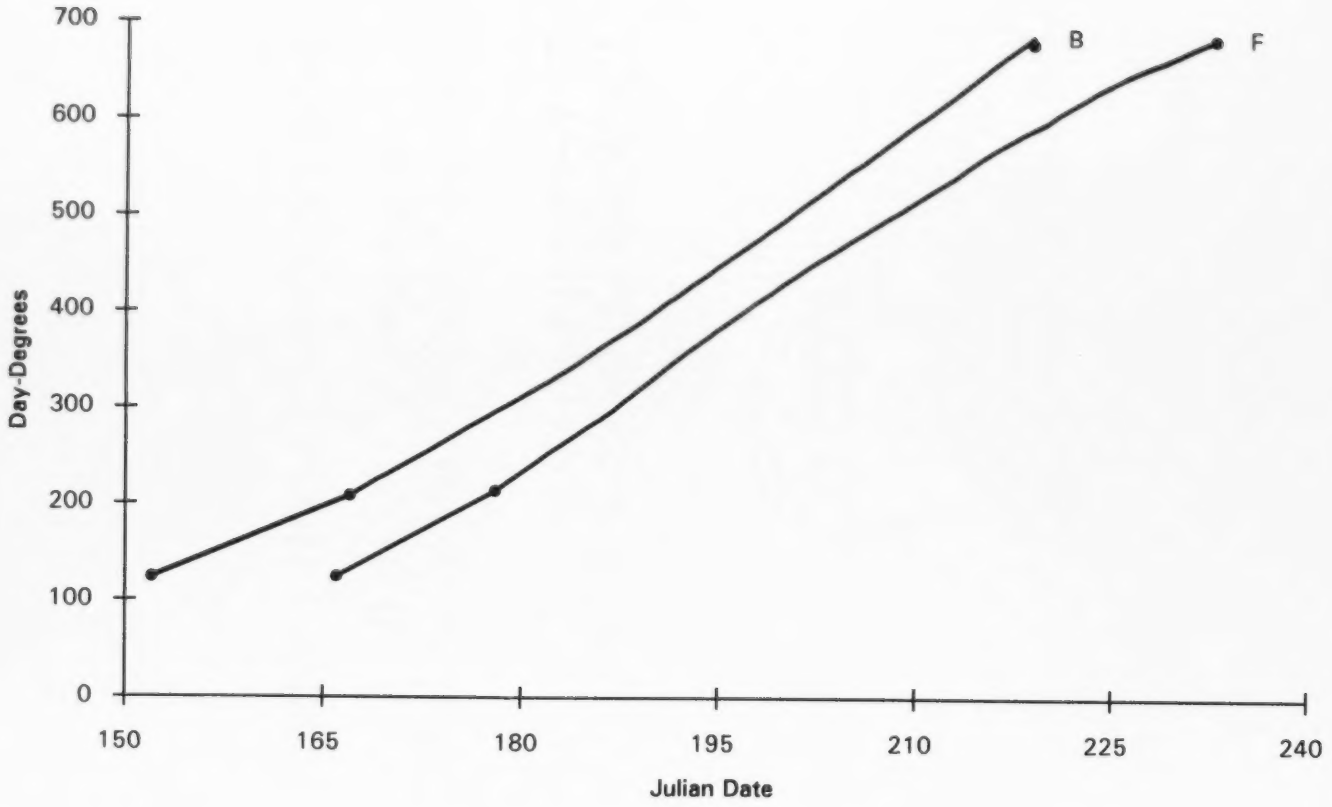

Figure III-7. Day-degree accumulation, Bowden (B) and Ft. Norman (F), three development intervals (Emergence, L2, L3-A).

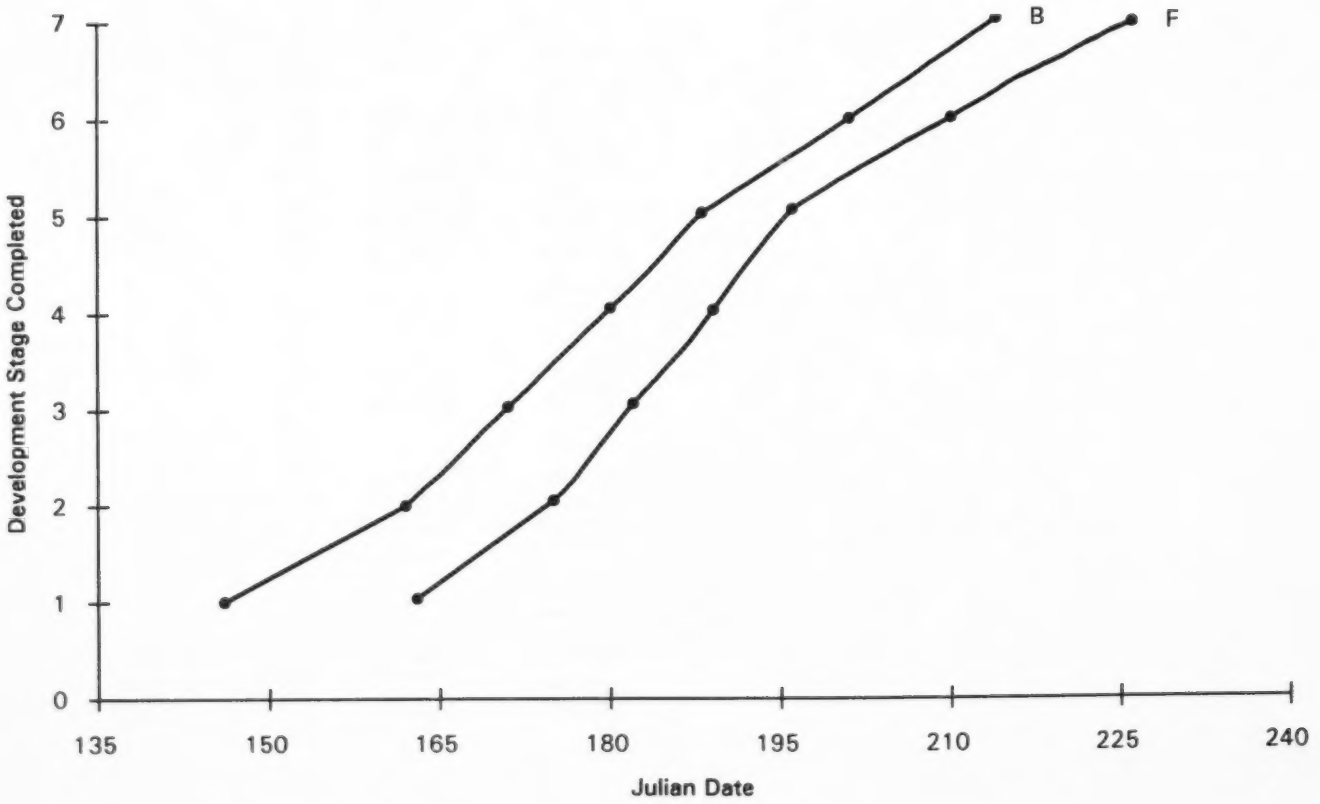

Figure III-8. Development accumulation, Bowden (B) and Ft. Norman (F), seven development intervals (Emergence, L2, L3, L4, L5, L6, PP).

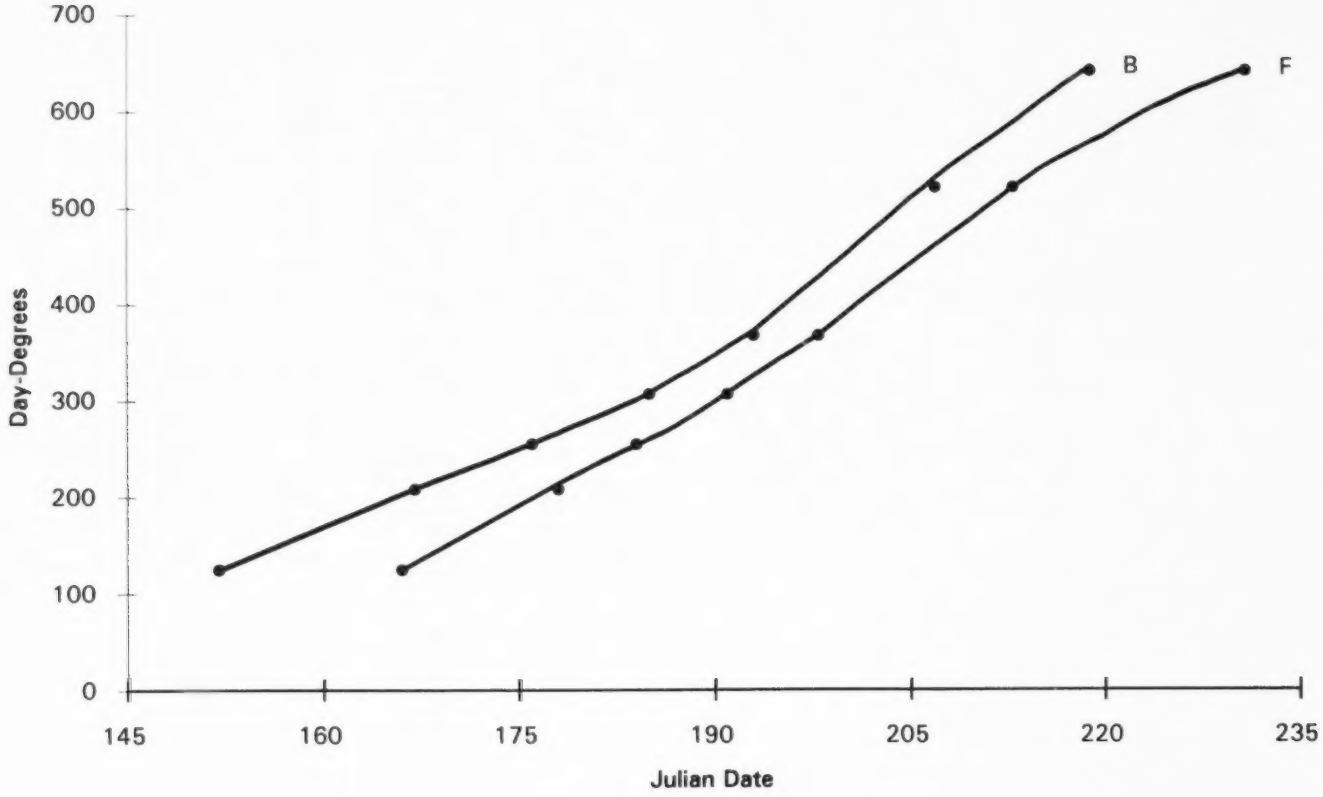

Figure III-9. Day-degree accumulation, Bowden (B) and Ft. Norman (F), seven development intervals (Emergence, L2, L3, L4, L5, L6, PP).

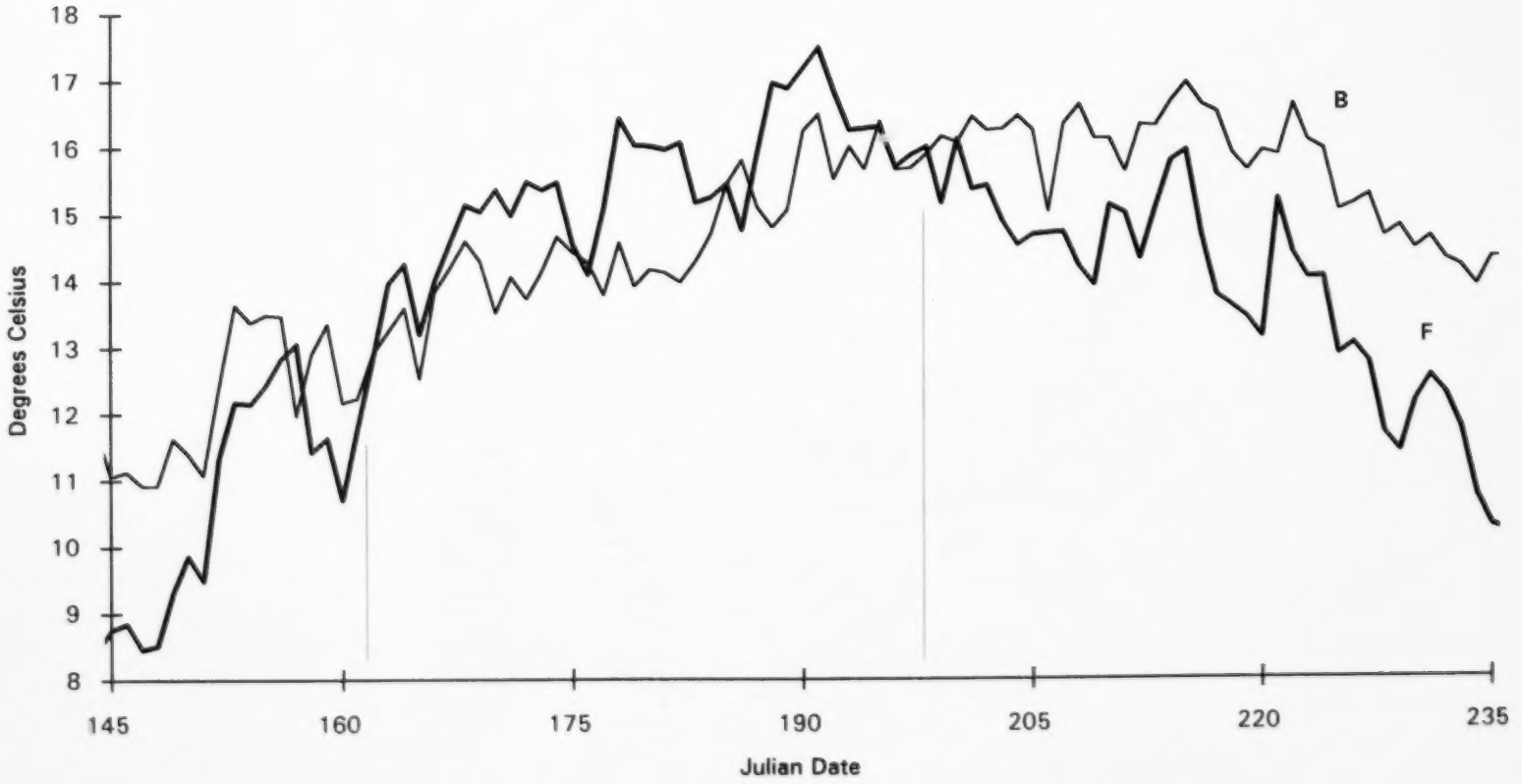

Figure III-10. Mean daily average temperatures, Bowden (B) and Ft. Norman (F).

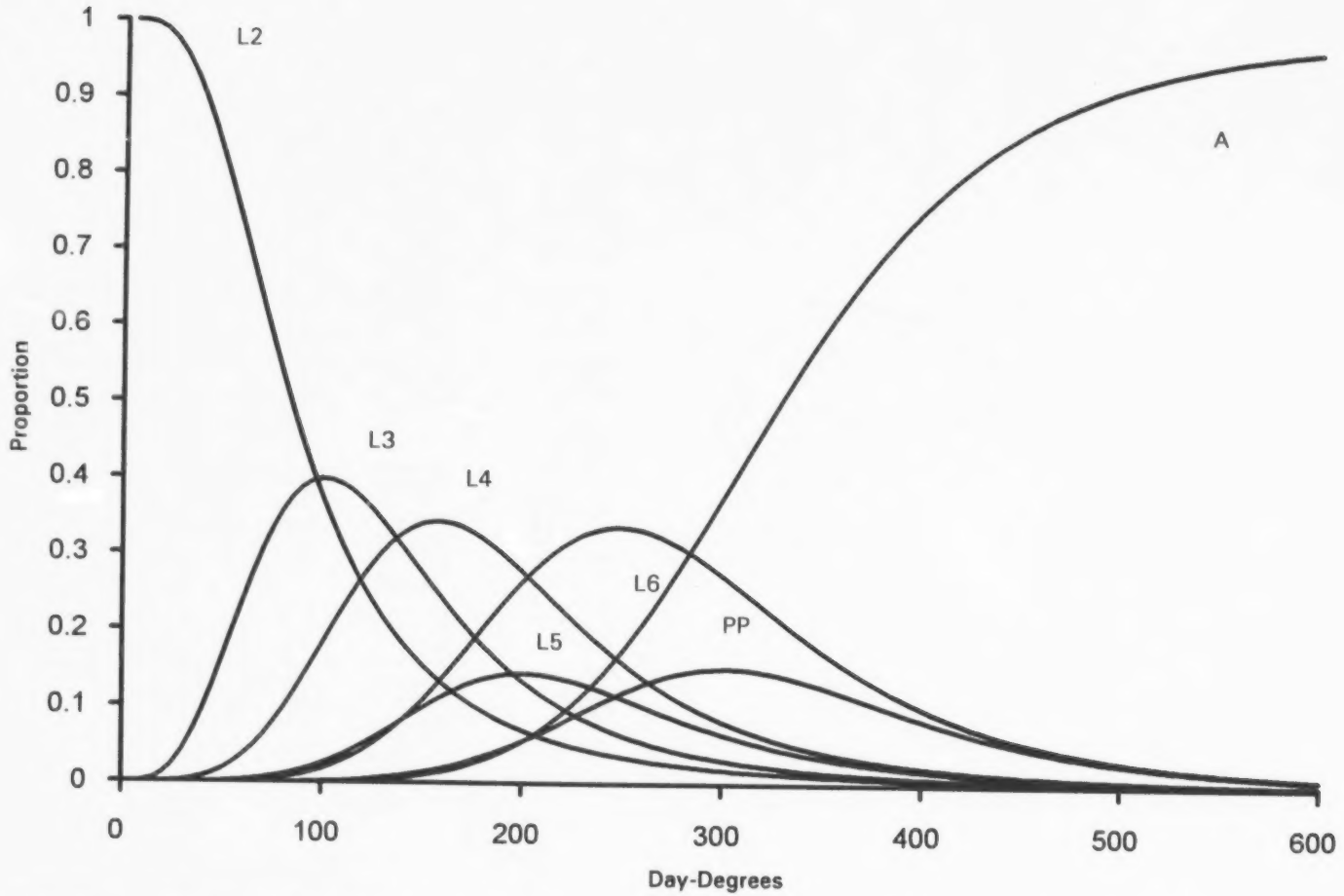

Figure III-11. Stochastic phenology model, Cypress Hills, 1993.

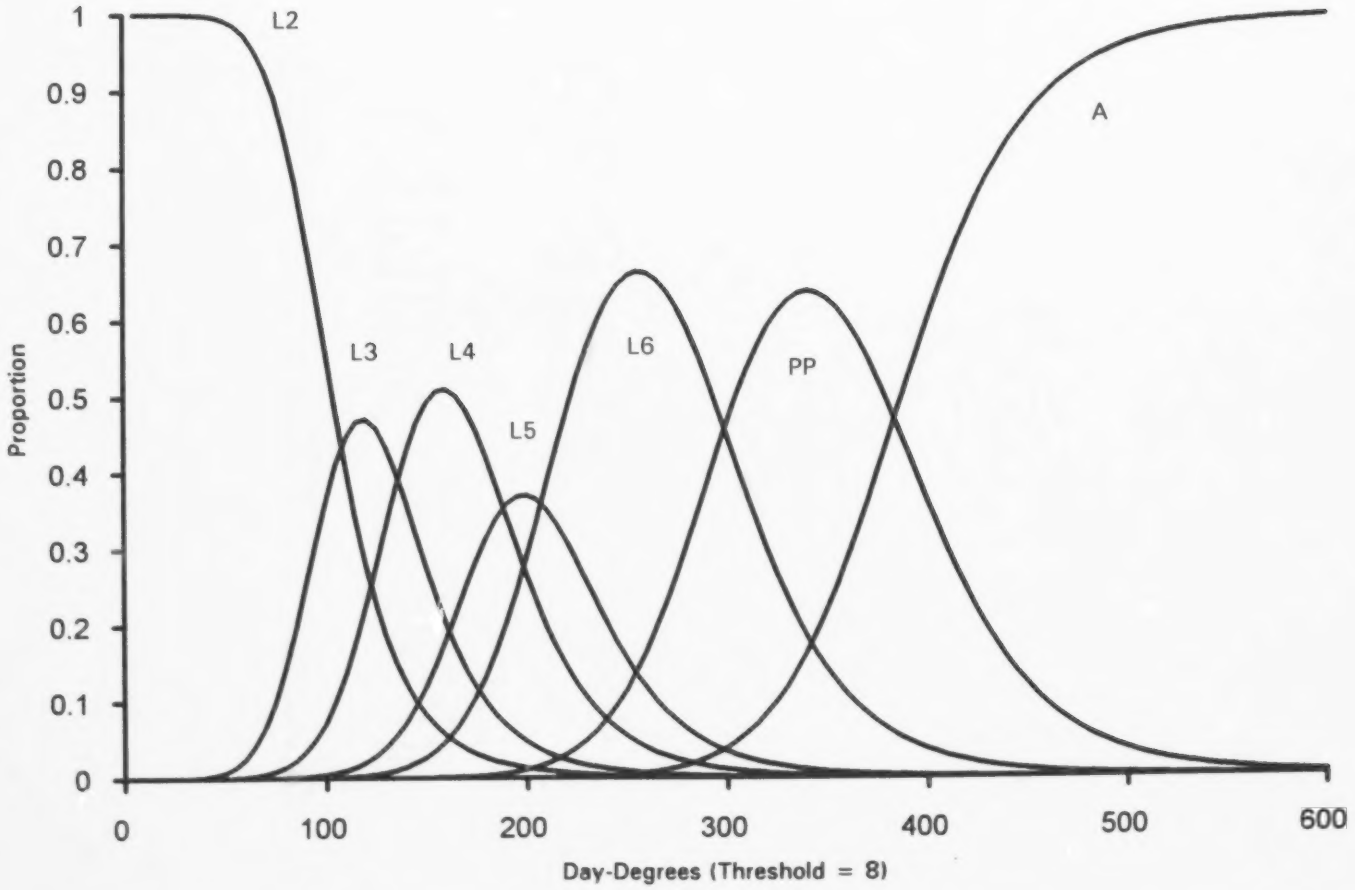

Figure III-12. Stochastic phenology model, Big River, 1993b.

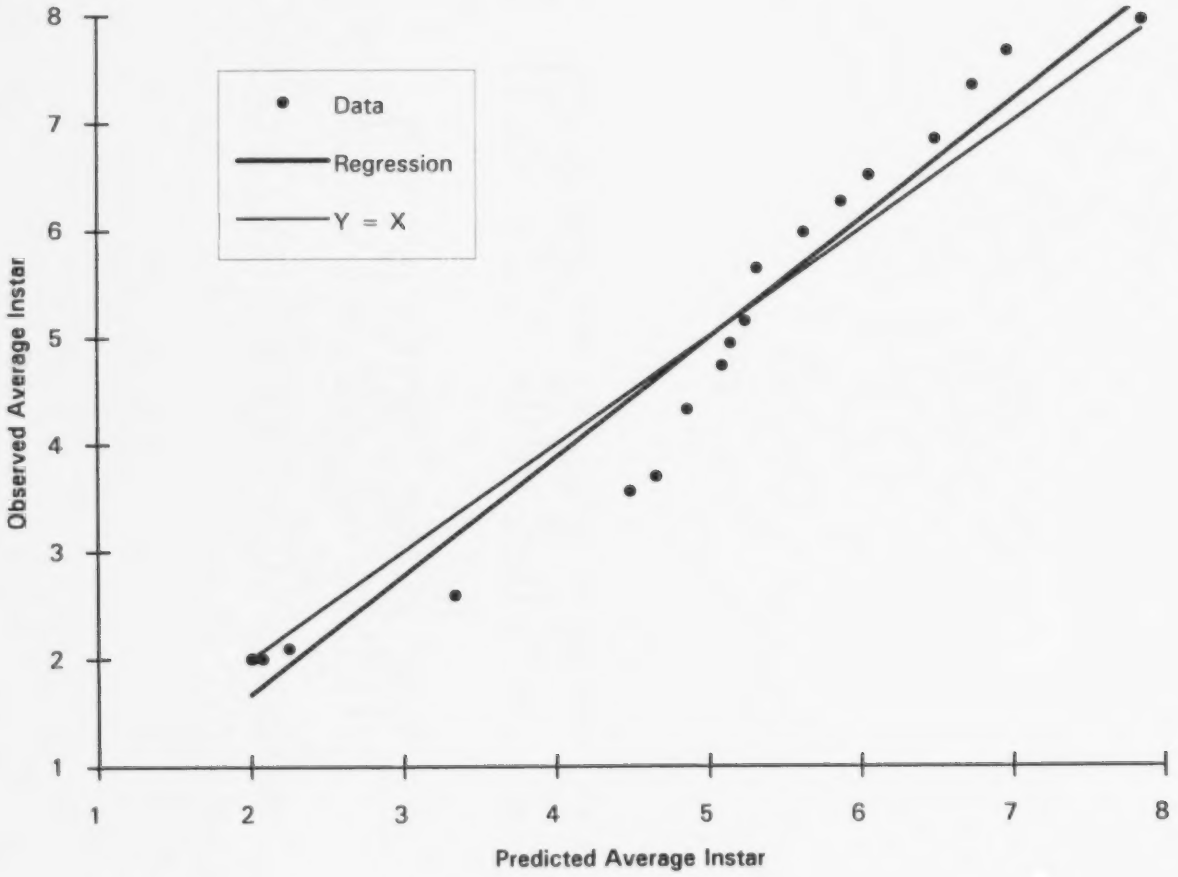

Figure III-13. Relationship between observed average instar, High Level, 1990, and predictions of Ontario 1989 model.

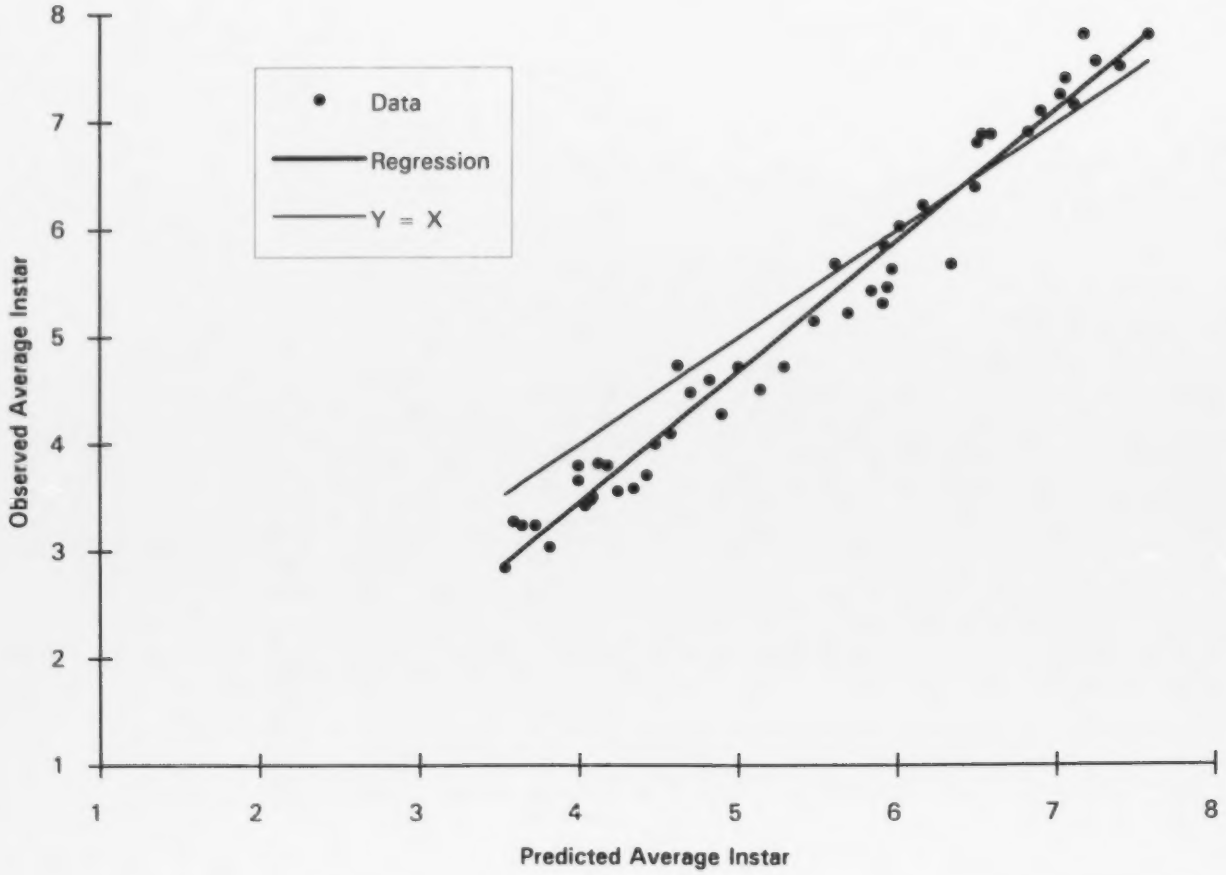

Figure III-14. Relationship between observed average instar, Big River, 1993b, and predictions of Ontario 1989 model.

Bibliography

Allen, J.C. 1976. A modified sine wave method for calculating degree-days. Environ. Entomol. 5: 388-396.

Arnold, C.Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Am. Soc. Hort. Sci. 74: 430-455.

Cameron, D.G., McDougall, G.A., and Bennett, C.W. 1968. Relation of spruce budworm development and balsam fir shoot growth to heat units. J. Econ. Entomol. 61: 857-858.

Cleary, B.D., and R.H. Waring. 1968. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. Can. J. Botany, 47: 167-173.

Dennis, B., W.P. Kemp, and R.C. Beckwith. 1986. Stochastic model of insect phenology: estimation and testing. Environ. Entomol. 15: 540-546.

Grisdale, D.G., and G.G. Wilson. 1991. Guidelines for rearing spruce budworm. Forest Pest Management Institute, Sault Ste. Marie, Ontario. 10 pp.

Harvey, G.T. 1985. The taxonomy of coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): a review. *In* Recent advances in spruce budworms research. Proceedings of the CANUSA Research Symposium, 16-20 Sept. 1984. Bangor, ME. C.J. Sanders, R.W. Stark, E.J. Mullens, and J. Murphy, eds. Can. For. Serv., Ottawa, Ont.

Higley, L.G., L.P. Pedigo, and K.R. Ostlie. 1986. Degday: a program for calculating degree-days, and assumptions behind the degree-day approach. Environ. Entomol. 15: 999-1016.

Hudes, E.S., and C.A. Shoemaker. 1984. Statistical comparison of spruce budworm (Lepidoptera: Tortricidae) Development on Balsam Fir and on Red and Black Spruce. Environ. Entomol. 13: 1602-1603.

Lamb, R.J. 1992. Development rate of *Acyrthosiphon pisum* (Homoptera: Aphidae) at low temperatures: implications for estimating rate parameters for insects.Environ. Entomol. 21(1): 10-19.

Logan, J.A., D.J. Wollkind, S.C. Hoyt, and L.K. Tanigoshi. 1976. An analytic model for the descriptioin of temperature-dependent rate phenomena in arthropods. Environ. Ent. 5: 1133-1140.

Lysyk, T.J. 1989. Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir. J. Econ. Entomol. 82(4): 1161-1168.

McGugan, B.M. 1954. Needle-mining habits and larval instars of the spruce budworm. Can. Ent. 86: 439-454.

Morris, R.F., and W.G. Fulton. 1970. Models for the development and survival of Hyphantria cunea in relation to temperature and humidity. Mem. Ent. Soc. Can. 70: 1-60.

Pruess, K.P. 1983. Day-degree methods for pest management. Environ. Entomol. 12: 613-619.

Régnière, J. 1987. Temperature-dependent development of eggs and larvae of *Choristoneura fumiferana* (Clem.)(Lepidoptera: Tortricidae) and simulation of its seasonal history. Can. Ent. 119: 717-728.

Régnière, J. 1982. A process-oriented model of spruce budworm phenology (Lepidoptera: Tortricidae). Can. Ent. 114: 811-825.

SAS Institute Inc. 1989. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2. Cary, NC:SAS Institute Inc., 846 pp.

Sharpe, P.J.H., and D.W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64: 649-670.

Shepherd, R.F. 1958. Factors controlling the internal temperatures of spruce budworm larvae, Choristoneura fumiferana (Clem.). Can. Journ. Zool. 36: 779-786.

Shepherd, R.F. 1961. A comparison of the developmental rates of one- and two-year cycle spruce budworm. Can. Ent. 93: 764-771.

Taylor, F. 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1-23.

Volney, W.J.A., and H. Cerezke. 1992. The phenology of white spruce and the spruce budworm in northern Alberta. Can. J. For. Res. 22: 198-205.

Volney, W.J.A., W.E. Waters, R.P. Akers, and A.M. Liebhold. 1983. Variation in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Ent. 115: 199-209.

Wellington, W.G. 1950. Effects of radiation on the temperatures of insectan habitats. Scient. Agric. 30: 209-234.

Conclusion

Three hypotheses were proposed to explain variation in thermal constants for the spruce budworm between sites in Ontario (Lysyk, 1989) and northern Alberta (Volney & Cerezke, 1992). The first was that clinal variation of intrinsic development rates over the gradient of latitude could account for apparent acceleration of development in the north. The second hypothesis was that regional bias in day-degree calculations was misrepresenting actual day-degree accumulations, tending to underestimate thermal constants of budworm development from field observations at northern latitudes. The final hypothesis was that linear thermal summation models do not accurately predict development at temperature extremes, and so contribute to discrepancies in thermal constants between populations. Tests of these three hypotheses failed to reveal effects which could account for lower thermal constants in northern populations of the spruce budworm.

Chapter two summarizes constant temperature rearing of spruce budworm from six populations across a gradient of latitude. Taylor's (1981) normal equation described the relationship between development rates and temperature. Model parameters did not reveal significant ($p<=.05$) differences in development rates for individuals from different regions. Development rates vary between instars as determined in a previous study (Régnière, 1982). Instar specific development rates may function in synchronizing development with phenological classes of host foliage (Volney & Cerezke, 1992). The large intrinsic variation in development rates of individuals may reflect variation in selection pressures. Taylor's predicted changes in rate parameters to accommodate a shorter growing season at

northern latitudes were not observed in this study.

The nonlinear rate model of Taylor (1981) was utilized in chapter three to model physiological time at two different latitudes. Relative development accumulations between the two sites was not affected by choice of a linear or nonlinear rate model. Thus, accumulation of development at temperature extremes does not account for variation in thermal constants. Early season accumulation of development below theoretical development thresholds may account for the fewer day-degrees accumulated in Ontario at the time of transition between second and third instars.

Bias in the sine method of day-degree calculations (Allen, 1976) also failed to explain observed differences in thermal constants of spruce budworm between regions. Bias does not appear to vary with daylength, as there is no trend in bias with increasing latitude. Bias equations are also variable depending on the particular data sets used to establish them. Variation between years was not taken into account in previous attempts to quantify regional bias (Allen, 1976; Pruess, 1983). The small variation in bias between locations and the larger variation between years makes the use of bias estimates in day-degree calculations unwarranted. Increased accuracy in defining day-degrees is unlikely to improve predictions of thermal summation models as they are estimates of development, and subject to variation between regions and years.

The stochastic phenology model (Dennis et al., 1986) was applied to additional observations of budworm phenology in western Canada. Variation in model parameters between years tended to obscure any trend in variation between sites at different latitudes. However, the difference in thermal constants between eastern and western Canada were supported

by the additional observations. Model variation should be considered in the context for which models are developed, which is usually a management operation which targets a specific stage in development.

In particular, application of *Bacillus thuringiensis* (B.t.) based insecticides must target the peak of sixth instar development. For many years earlier instars were targeted as it was believed this would give optimal foliage protection. Volney and Cerezke (1992) suggested that targeting earlier instars was not viable in northern Alberta because of their rapid development time and habit of sheltering within developing shoots by anchoring the budcap with silk. The sixth instar is exposed and consumes the most foliage, increasing the probability that a lethal dose of B.t. will be ingested. Optimal population suppression should result as natural mortality factors are free to affect earlier instars, but it was believed that foliage protection would be compromised. Nealis et al.(1992) found that parasitoids were conserved in late spray treatments and that overall population reductions were greater in these treatments. As a result, foliage protection was similar for both early and late sprays. It is likely that future applications of this insecticide will target the sixth instar, but it took many years of trials before this optimum window of application was determined.

Although the sixth instar is targeted, factors such as precipitation affect application of B.t., and applications occur over a period of days. Thus, exact predictions of date to peak sixth instar development may not be necessary as long as estimates are not conservative, which could allow the window of opportunity to pass by. Field observations of phenology are required for such management procedures, and may be used in conjunction with phenology models to predict

development. As the age structure of the budworm population is determined closer to the targeted age structure, the precision of phenology model predictions increase.

As management procedures are constantly being refined, so too are the phenological models which are used in management operations. Similarly, it may take many years of refinement before fundamental changes in phenological modelling occur. Refinements in phenology models based on thermal summation are not likely to improve predictions of development. Higley et al. (1986) note that acceptable error in the predictions of phenology models for pest management may be 15%. Thus refinements of day-degree calculations from an application perspective are inconsequential. This also applies to refinements in thermal constants derived from laboratory rearing, such as basing them on development rates under fluctuating rather than constant temperatures (Eubank, et al., 1973). Even considering the large variation of thermal summation models between years, they are useful as a guide to development, which is evident in their continued use by botanists and entomologists. The discrepancies in predictions for different regions should lead to refinement of phenology models in terms of variables considered. This leads to further research into the factors governing development processes.

The observed differences in budworm thermal constants for different regions does not appear to be explained by temperature based processes. Effects of photoperiod on budworm development in different regions have not yet been investigated. Morris & Foulton (1970) demonstrate that insect feeding patterns are affected by photoperiod. Longer daylengths in the north could result in budworms consuming more foliage on a given day, independent of relative

temperatures experienced at northern and southern sites. Another factor to consider is light intensity. Budworms experience temperatures above ambient, within their microhabitats. The degree of this temperature differential is dependent on intensity of incident light (Shepherd, 1958), and average hours of bright sunshine per day vary across regions. Future investigations of spruce budworm phenology might consider effects of photoperiod and light intensity on development accumulation.

Bibliography

Allen, J.C. 1976. A modified sine wave method for calculating degree-days. Environ. Entomol. 5: 388-396.

Dennis, B., W.P. Kemp, and R.C. Beckwith. 1986. Stochastic model of insect phenology: estimation and testing. Environ. Entomol. 15: 540-546.

Eubank, W.P., J.W. Atmar, and J.J. Ellington. 1973. The significance and thermodynamics of fluctuating versus static thermal environments on *Heliothis zea* egg development rates. Environ. Entomol. 2: 491-496.

Higley, L.G., L.P. Pedigo, and K.R. Ostlie. 1986. Degday: a program for calculating degree-days, and assumptions behind the degree-day approach. Environ. Entomol. 15: 999-1016.

Lysyk, T.J. 1989. Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir. J. Econ. Entomol. 82(4): 1161-1168.

Morris, R.F., and W.G. Fulton. 1970. Models for the development and survival of Hyphantria cunea in relation to temperature and humidity. Mem. Ent. Soc. Can. 70: 1-60.

Nealis, V.G., K. van Frankenhuyzen, and B.L. Cadogan. 1992. Conservation of spruce budworm parasitoids following application of *Bacillus thuringiensis* var. *Kurstaki* Berliner. Can. Ent. 124: 1085-1092.

Pruess, K.P. 1983. Day-degree methods for pest management. Environ. Entomol. 12: 613-619.

Régnière, J. 1982. A process-oriented model of spruce budworm phenology (Lepidoptera: Tortricidae). Can. Ent. 114: 811-825.

Shepherd, R.F. 1958. Factors controlling the internal temperatures of spruce budworm larvae, Choristoneura fumiferana (Clem.). Can. Journ. Zool. 36: 779-786.

Taylor, F. 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1-23.

Volney, W.J.A., and H. Cerezke. 1992. The phenology of white spruce and the spruce budworm in northern Alberta. Can. J. For. Res. 22: 198-205.